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Diversity and phylogeny of yeasts in various habitats of the Arctic and Antarctic regions, with descriptions of one new family, five new genera and eighteen new species

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Abstract: The Arctic and Antarctic regions are characterized by low temperatures, high solar irradiation, and successive freezing and thawing cycles. To date, 57 yeast species belonging to 24 genera have been identified as novel taxa initially isolated from Arctic and Antarctic environments. This study comprehensively explored yeast diversity in diverse habitats, including soil, freshwater, seawater, lichens, mosses, vascular plants, dung, feathers, algae, and mushrooms, in the Ny-Ålesund (Arctic) and Fildes regions (Antarctica). Over the past decade, a total of 406 samples were collected, resulting in the isolation of 2215 yeast strains. Molecular analysis revealed 2150 yeast strains across 80 known species in 36 genera. Remarkably, 65 yeast strains – 33 from Antarctica and 32 from the Arctic – were classified as novel taxa. Based on phylogenetic and phenotypic analyses, we described 18 new basidiomycetous yeast species across two classes: *Tremellomycetes* within *Agaricomycotina* and *Microbotryomycetes* within *Pucciniomycotina*. Furthermore, we proposed the establishment of one new family, *Pricozymaceae*, and five new genera, including *Pricozyma*, *Xiangyanghongia*, *Chioneozyma*, *Skadia*, and *Xuelongia*. In summary, this study revealed a rich diversity of yeast species in the Arctic and Antarctica, identifying 98 species across 40 genera, 22 families, 12 orders, four classes, and two phyla, many of which were previously unknown. Novel species described include: *Chioneozyma fusiformis*, *Chioneozyma ovata*, *Dioszegia frigidiaquatica*, *Dioszegia dongchenii*, *Fellozyma antarctica*, *Genolevuria ovata*, *Glaciozyma ellipsoidea*, *Glaciozyma elongata*, *Phaeotremella nansenii*, *Phaeotremella polaris*, *Pseudotremella lichenophila*, *Piskurozyma viscida, Pricozyma crymophila*, *Skadia corniformis*, *Skadia rubropurpurea*, *Xiangyanghongia terricola*, *Xuelongia filamentosa*, and *Yunzhangia cylindrica*.

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INTRODUCTION

The polar regions, comprising the Arctic and Antarctica, are vital to Earth's biosphere, covering nearly 14 % of its surface (Kosek *et al.* 2016). Characterized by extreme conditions such as low temperatures, high solar irradiation, and repeated freezing-thawing cycles, these regions demand unique adaptations from resident microbes, including bacteria and fungi (Robinson 2001, Buzzini *et al.* 2012, Lauritano *et al.* 2020). Yeasts, a unicellular type of fungi, display a remarkable array of adaptive mechanisms, thriving in diverse ecological niches with varied nutritional requirements (Buzzini *et al.* 2017). Previous studies indicated that yeasts have a higher tolerance for cold stress than bacteria (Margesin *et al.* 2003), with cold-active enzymes from polar yeasts showing significant industrial potential (Ramli *et al.* 2011, Ramli *et al.* 2013, Bialkowska *et al.* 2018, Kumari *et al.* 2021, Parvizpour *et al.* 2021). Through these enzymes, yeasts are crucial to nutrient cycling and organic matter mineralization in the polar regions, where nutrient availability is constrained (Ludley & Robinson 2008, Fernández *et al.* 2017, Martorell *et al.* 2019). Although polar yeast enzymes demonstrate considerable biotechnological potential (Kim *et al.* 2014), current knowledge regarding yeast communities across polar ecological niches remains limited.

A total of 119 yeast species thriving in the extreme habitats of Antarctica and sub-Antarctica regions were identified (Buzzini *et al.* 2017). Among these, 25 species were ascomycetous yeasts, and 94 species were basidiomycetous yeasts. Soil and organic materials served as primary growth substrates for these yeasts. Similarly, in the Arctic and sub-Arctic regions, nine species were ascomycetous yeasts, and 53 species were basidiomycetous yeasts. These yeasts primarily grew on soil, organic materials, and ice cores (Buzzini *et al.* 2017). According to the classification standard of Gounot (1986), cold-adapted microbes are categorized

into psychrophiles and psychrotrophs. Both can thrive at 0 °C; however, psychrophiles have a maximal growth temperature of 20 °C, unlike psychrotrophs, which can grow above 20 °C. Species from psychrophilic or psychrotrophic genera such as *Glaciozyma*, *Mrakia*, and *Phenoliferia* were frequently isolated in both the Arctic and Antarctica (Duarte *et al.* 2016, Ferreira *et al.* 2019, Tsuji *et al.* 2019a). Overall, basidiomycetous yeasts were more prevalent than ascomycetous yeasts in both polar regions.

Documentation of yeasts inhabiting cold environments is scarce, as highlighted by Boekhout *et al.* (2022). By 2023, only 57 yeast species across 24 genera were identified as novel taxa from the Arctic and Antarctic regions (Table S1). Among these, Antarctica was the initial isolation site for 39 species (di Menna 1966, Fell & Phaff 1967, Fell & Hunter 1968, Fell *et al.* 1969, Fell 1970, Fell & Statzell 1971, Fell *et al.* 1973, Vishniac & Hempfling 1979, Vishniac 1985, Vishniac & Kurtzman 1992, Montes *et al.* 1999, Scorzetti *et al.* 2000, Thomas-Hall & Watson 2002a, b, Guffogg *et al.* 2004, Xin & Zhou 2007, Connell *et al.* 2010, Thomas-Hall *et al.* 2010, Turchetti *et al.* 2011, Laich *et al.* 2013, Kachalkin 2014, Laich *et al.* 2014, Selbmann *et al.* 2014, Zhang *et al.* 2014, Trochine *et al.* 2017, Tsuji *et al.* 2017, de Garcia *et al.* 2020, Touchette *et al.* 2022), the Arctic for 22 species (Golubev 1998, Vishniac 2002, Margesin & Fell 2008, Vishniac & Takashima 2010, de Garcia *et al.* 2012, Singh *et al.* 2014, Tsuji *et al.* 2018a, b, Turchetti *et al.* 2018, Tsuji *et al.* 2019a, b, Pontes *et al.* 2020, Perini *et al.* 2021), and four species were found in both regions (di Menna 1966, Turchetti *et al.* 2015, Yurkov *et al.* 2015, de Garcia *et al.* 2020). This accounts for only 2.9 % of the total yeast species identified by 2022 (1958 species), according to The Yeasts Trust Database (https://theyeasts.org). Nonetheless, the identification and characterization of new yeast genera and species have increased globally since the early 21st century (Boekhout *et al.* 2022). While only 16 new yeast species were reported from polar regions before 2000, an additional 39 species have been validly described since 2000 (Table S1).

Various species concepts have been developed and refined within the taxonomic studies of yeasts. Boekhout *et al.* (2021) highlighted three key concepts: (1) the phenotypic species concept and its molecular counterpart, the genetic species concept; (2) the biological species concept; and (3) the phylogenetic species concept, which includes genealogical concordance phylogenetic species recognition. These concepts emphasize different aspects of eukaryotic life. The phenotypic species concept, focusing on morphology and physiology, has traditionally been instrumental in early yeast taxonomy (Giraud *et al.* 2008, Boekhout *et al.* 2021). The biological species concept, which centers on sexual reproduction within populations, is considered less suitable for classifying anamorphic yeasts (Giraud *et al.* 2008, Boekhout *et al.* 2021). Conversely, the phylogenetic species concept, relying on nucleotide sequences or genomes, plays an important role in the identification and classification of yeast species (Taylor *et al.* 2000). In this study, the phylogenetic species concept was employed for defining new yeast species and, consequently, establishing new yeast genera, as outlined by Lachance (2018).

Climate warming significantly impacts polar ecosystems by altering weather patterns, reducing sea ice cover, melting extensive permafrost areas, and affecting vegetation and microbial communities (Tape *et al.* 2006, Deslippe *et al.* 2012, Yergeau *et al.* 2012, Biskaborn *et al.* 2019). These ecological shifts highlight the need for a comprehensive exploration of yeast diversity in the diverse habitats of the polar regions. This study aims to explore the distribution and diversity of yeast species across a wide range of habitats, including soil, freshwater, seawater, lichens, mosses, vascular plants, dung, feathers, marine and green algae, and mushrooms, in the Arctic and Antarctic regions. Moreover, we have identified 18 new yeast species using morphological and phylogenetic analyses. Our results significantly enhance the understanding of yeast diversity within polar ecosystems during rapid climate change.

MATERIALS AND METHODS

Study sites and sample collection

In the Arctic, the sampling site was located in the Ny-Ålesund region (78°55'N, 11°56'E), situated on the Brøgger Peninsula along the west coast of Spitsbergen, Svalbard archipelago (Fig. S1). This region experienced an average temperature of -4.2 °C from 1969 to 2013, with annual precipitation averaging 415.5 mm (López-Moreno *et al.* 2016). Samples were collected from 10 distinct habitats between July and September in 2013, 2018, 2019, and 2023 (Fig. 1). In Antarctica, the sampling location was chosen in the Fildes region (62°12′S, 58°57′W), which includes the Fildes Peninsula and nearby islands at the southwestern tip of King George Island in the South Shetland Islands (Fig. S1). The average annual air temperature was -2.2 °C between 2000 and 2012, with precipitation varying from 350 to 500 mm annually (Michel *et al.* 2014, Øvstedal & Lewis Smith 2001). Samples were collected from nine habitats in January of 2012, 2016, 2017, and 2018 (Fig. 2).

Yeast isolation

The organic samples (lichens, mosses, vascular plants, mushrooms, green algae, and marine algae) were meticulously cleaned with sterile deionized water, dried with sterile filter paper, fragmented into small pieces using sterile scissors, and evenly distributed onto Petri dishes containing nutrient media. Feather samples were aseptically cut into small pieces and directly inoculated onto the media without further processing (Singh *et al.* 2016). Soil and dung samples were either directly sprinkled onto the media using sterile tweezers or dispersed in sterile deionized water before being inoculated on agar plates (Sugita *et al.* 2005, Ding *et al.* 2016). Yeasts from freshwater and seawater samples were isolated and cultivated using membrane filtration techniques as described by Zhang *et al.* (2017).

Potato dextrose agar (PDA) was prepared by boiling 200 g potato extract, supplemented with 20 g glucose and 15 g agar per litre. This medium was then used for the isolation of yeasts from terrestrial samples. Some samples were simultaneously cultured on Czapek Dox agar (CZA), which contains 3 g potassium nitrate, 1 g dipotassium hydrogen phosphate, 0.5 g magnesium sulphate, 0.5 g potassium chloride, 0.01 g ferrous sulphate, 30 g sucrose, and 15 g agar per litre. For marine-related samples, marine agar supplemented

with 2 % (w/v) glucose (Difco, MA) was used. Streptomycin sulphate (50 mg/L) and tetracycline hydrochloride (50 mg/L) were added to all media to inhibit bacterial growth. The Petri dishes were incubated at 4 °C or 12 °C for 6–8 wk, with colony growth monitored weekly. Primitive yeast or yeast-like colonies were isolated on PDA slants. All pure cultures were preserved with 20 % (v/v) glycerol at -80 °C for long-term storage in our laboratory. The novel yeast strains were deposited in the China Pharmaceutical Culture Collection (CPCC), and the type strains were also deposited in the CBS culture collection (CBS) at the Westerdijk Fungal Biodiversity Institute.

DNA extraction, PCR amplification, and sequencing

Genomic DNA was extracted using the modified CTAB method (Cubero *et al.* 1999) or Chelex-100 chelating resin (Walsh *et al.* 1991, Porebski *et al.* 1997). The internal transcribed spacer, including the 5.8S rDNA (ITS), and the D1/D2 domains of the large subunit rDNA (D1/D2), were amplified

Fig. 1. A. Overview of the Ny-Ålesund Region (Arctic). **B.** Glacier and meltwater. **C.** Stream. **D.** Lichen. **E.** Vascular plant. **F.** Moss and mushroom. **G.** Marine alga. **H.** Reindeer. **I.** Reindeer dung. **J.** Arctic terns. **K.** Feather.

using polymerase chain reactions with primer sets ITS1/ITS4 or ITS1F/ITS4 and NL1/NL4 for the ITS and D1/D2 regions respectively, and sequenced using the same primer sets (White *et al.* 1990, Gardes & Bruns 1993, O'Donnell 1993). Sequences of 18S rDNA and four protein-coding genes – translation elongation factor 1-α (*TEF1*), RNA polymerase II largest subunit (*RPB1*), RNA polymerase II second largest subunit (*RPB2*), and mitochondrial cytochrome b (*CYTB*) – were also amplified following the methods outlined for the phylogeny of basidiomycetous yeast taxa by Liu *et al.* (2015) and Wang *et al.* (2015). The primers for amplification and sequencing are listed in Table S2, and PCR assays were conducted according to the protocols described by White *et al.* (1990), Rehner & Buckley (2005), Wang *et al.* (2014), and Biswas *et al.* (2001). The sequencing was performed by Sangon Biotech (Shanghai) Co., Ltd. The sequences generated in this study have been deposited in GenBank and are listed in Table 1.

Fig. 2. A. Overview of the Fildes Region (Antarctica). **B.** Glacier. **C.** Lake. **D.** Seawater. **E.** Lichen vegetation. **F.** Moss vegetation. **G.** Green alga and moss. **H.** Vascular plant. **I.** Penguin. **J.** Penguin dung.

Molecular analyses

In this study, the ITS region and D1/D2 domains served as the primary basis for yeast strain identification. While identification benchmarks proposed by Fell et al. (2000), Kurtzman (2014), Vu et al. (2016), and Boekhout *et al.* (2021) were considered, they were not strictly followed. Strains that could not be directly identified through similarity comparison of ITS or D1/D2 sequences were further analysed using concatenated ITS-D1/D2 phylogenetic methods, supplemented with additional genes (*TEF1*, *RPB1*, *RPB2*, *CYTB*) when necessary.

Phylogenetic analyses of the novel yeast species within the *Tremellomycetes* and *Microbotryomycetes* classes primarily utilized the methodologies developed by Liu *et al.* (2015) and Wang *et al.* (2015). New sequences were assembled using the SeqMan module of Lasergene v. 7.1.0 (DNASTAR) (Burland 1999) and aligned with reference sequences from NCBI's nucleotide database using MAFFT Windows all-in-one v. 7.471, employing the G-INS-i algorithm for each locus (Katoh & Standley 2013). Introns within protein-coding genes and 18S rDNA were excised prior to alignment (Black 2003). Ambiguities in the alignments were manually corrected with MEGA v. 7 (Kumar *et al.* 2016). Alignments for each locus were concatenated using PhyloSuite v. 1.1.16 (Zhang *et al.* 2020) The GTR+GAMMA+I model was chosen for maximum likelihood and Bayesian inference analyses, with partitions for each independent locus. This study constructed the seven-gene phylogenetic relationships for novel species, serving as primary references for their delineation. Additionally, due to the absence of protein-coding genes in some closely related species, concatenated ITS (including 5.8S rDNA) and D1/D2 phylogenies from ex-type strains or strains used in this study, along with closely related sequences from GenBank, were also utilized for novel species identification. Maximum likelihood analysis was performed with RAxML-HPC v. 8.2.x, including 1000 bootstrap resamples (Stamatakis 2014). Bayesian inference was executed on the CIPRES Science Gateway using MrBayes v. 3.2.6, with runs of 5 M to 20 M generations, employing two simultaneous runs and four chains for taxa within *Tremellomycetes*, and fifteen chains for taxa within *Microbotryomycetes* (Perini *et al.* 2021). The chain swapping temperature was set at 0.1, with sampling every 1000 generations until the average standard deviation of split frequencies fell below 0.01. The initial 25 % of sampled trees were discarded as burn-in (Miller *et al.* 2010, Ronquist *et al.* 2012). Phylogenetic trees were visualized using FigTree v. 1.4.4, with nodes supported by bootstrap values > 70 % or posterior probabilities > 0.9 considered well-supported. The phylogenetic alignments and trees, based on the seven-gene analysis of *Agaricomycotina* and *Pucciniomycotina*, have been deposited in TreeBASE (accession number: S31813).

Phenotypic characterization

The morphological, physiological, and biochemical characteristics of the novel taxa were assessed using the standard methods established by Kurtzman *et al.* (2011). Yeast cells were cultured on Yeast Malt (YM) agar (Difco) at temperatures ranging from 4 °C to 37 °C, and colony morphology was documented after 4 wk. Fermentation abilities were evaluated using glucose, lactose, galactose, sucrose, maltose, and raffinose in liquid media. Urea hydrolysis was tested on Christensen's urea agar, and the Diazonium Blue B reaction was assessed on an agar medium. The potential for sexual reproduction and hyphae formation in novel yeast strains was investigated over two months on YM agar, Potato Dextrose agar (PDA), corn meal agar (CMA), sucrose-yeast extract agar (SYA), and malt extract agar (MEA), with microscopic observations made bi- or tri-weekly. For scanning electron microscopy (SEM), yeast cell preparation followed the method described by Feng *et al.* (2021), using a cold field-emission SEM (Hitachi SU8010, Tokyo, Japan) for observation.

RESULTS

Diversity of yeasts in the Arctic and Antarctica

In this comprehensive study, we isolated 1102 yeast strains from 234 samples collected in the Arctic and 1113 strains from 172 samples in Antarctica. Among the 2215 total isolates, basidiomycetous yeasts were predominant, with 2102 strains accounting for approximately 95 % of the total, demonstrating a significant dominance over ascomycetous taxa. Following the phylogenetic identification standards previously outlined, 2150 strains were identified as 80 known species (Table 2). Additionally, 65 strains of *Basidiomycota* – 33 from Antarctica and 32 from the Arctic – were identified as 18 novel taxa (Table 1).

This study identified a total of 98 species across 40 genera, 22 families, 12 orders, four classes, and two phyla. Among these, 34 species were isolated from both the Arctic and Antarctica, highlighting the widespread distribution of some yeast species. Furthermore, 31 species were isolated exclusively from Antarctica, while 33 species were found solely in the Arctic, indicating unique regional distributions. Interestingly, 15 known species had not been previously isolated from either polar region (Table 2). In terms of prevalence, *Vishniacozyma victoriae*, *Goffeauzyma gilvescens*, and *Mrakia gelida* were identified as the most common species in the Arctic, with some species isolated from at least five different habitats. Similarly, in Antarctica, *Vishniacozyma victoriae*, *Phenoliferia psychrophila*, and *Phenoliferia glacialis* were the most frequently isolated species, along with other species that showed habitat specificity.

The yeasts identified in this study are characterized by their psychrophilic or cold-adapted nature, including genera such as *Cryolevonia*, *Glaciozyma*, *Phenoliferia*, *Leucosporidium*, as well as species like *Vishniacozyma victoriae*, *Cystobasidium laryngis*, and *Goffeauzyma gilvescens*. The study also highlighted the habitat-specific or geographical limitations of certain species, such as three *Metschnikowia* species: *Metschnikowia australis* isolated exclusively from Antarctic seawater, and *Metschnikowia bicuspidata* and *Metschnikowia zobellii* from Arctic seawater and marine algae.

Phylogenetic analysis of novel yeast species

A comprehensive analysis generated sequences for seven loci, including 65 sequences each for the ITS region and D1/

Table 1. Information on species, strain numbers, sources, and sequence accession numbers for the 18 new yeast species identified in this study.

Species	Strain	Locality	Habitat	GenBank accession number						
				ITS	D1/D2	18S	*RPB1*	*RPB2*	*TEF1*	*CYTB*
Dioszegia dongchenii sp. nov.	CPCC 300431^{T}	Arctic	Vascular plant	OM980462	OM980551	ON007473	ON188994	ON188874	ON188919	ON189031
	CPCC 300073	Antarctica	Vascular plant	OQ526215	OQ525991	–	–	–	–	–
Dioszegia frigidiaquatica sp. nov.	CPCC 300401^{T}	Arctic	Seawater	OM980401	OM980490	ON007427	ON188955	ON188833	ON188891	ON189000
	CPCC 300271	Antarctica	Freshwater	OM980399	OM980488	ON007429	ON188957	–	ON188893	ON189002
	CPCC 300379	Arctic	Seawater	OM980400	OM980489	ON007428	ON188956	–	ON188892	ON189001
Fellozyma antarctica sp. nov.	CPCC 300301^{T}	Antarctica	Lichen	OM980453	OM980542	ON007462	–	ON188865	ON188922	ON189024
	CPCC 300300	Antarctica	Lichen	OM980452	OM980541	ON007461	–	ON188864	ON188921	ON189023
	CPCC 300418	Antarctica	Moss	OM980454	OM980543	ON007463	ON188987	ON188866	ON188923	–
Glaciozyma ellipsoidea sp. nov.	CPCC 300473^{T}	Arctic	Soil	OM980437	OM980526	ON007454	–	ON188853	ON188932	ON189017
	CPCC 300395	Arctic	Soil	OM980436	OM980525	ON007453	–	–	ON188912	–
Glaciozyma elongata sp. nov.	CPCC 300077^{T}	Antarctica	Soil	OM980431	OM980520	ON007451	–	ON188851	ON188910	ON189015
	CPCC 300449	Antarctica	Soil	OM980432	OM980521	ON007452	–	ON188852	ON188911	ON189016
	CPCC 300492	Antarctica	Soil	OM980434	OM980523	–	–	–	–	–
	CPCC 300503	Antarctica	Soil	OM980435	OM980524	ON007474	–	–	–	–
	CPCC 300511	Antarctica	Soil	OM980433	OM980522	–	–	–	–	–
Phaeotremella nansenii sp. nov.	CPCC 300414^{T}	Arctic	Lichen	OM980392	OM980481	ON007424	ON188952	ON188830	ON188889	ON188997
	CPCC 300496	Arctic	Lichen	OM980393	OM980482	ON007425	ON188953	ON188831	ON188890	ON188998
Phaeotremella polaris sp. nov.	CPCC 300468^{T}	Arctic	Lichen	OM980394	OM980483	ON007426	ON188954	ON188832	ON188929	ON188999
	CPCC 300298	Antarctica	Moss	OM980397	OM980486	ON007466	–	ON188868	ON188917	ON189026
	CPCC 300490	Arctic	Lichen	OM980395	OM980484	–	–	–	–	–
	CPCC 300501	Arctic	Lichen	OM980396	OM980485	–	–	–	–	–
	CPCC 300516	Arctic	Lichen	OM980398	OM980487	ON007471	ON188992	ON188872	ON188927	ON189029
Chioneozyma ovata sp. nov.	CPCC 300339^{T}	Antarctica	Soil	OM980450	OM980539	ON007460	ON188986	ON188863	ON188920	ON189022
	CPCC 300081	Antarctica	Lichen	OM980448	OM980537	ON007458	ON188980	ON188857	ON188915	–
	CPCC 300302	Antarctica	Lichen	OM980444	OM980533	–	ON188984	ON188861	ON188916	–
	CPCC 300493	Antarctica	Soil	OM980449	OM980538	–	–	–	–	–
	CPCC 300500	Antarctica	Lichen	OM980451	OM980540	–	–	–	–	–
Chioneozyma fusiformis sp. nov.	CPCC 300299^{T}	Antarctica	Lichen	OM980446	OM980535	ON007459	ON188982	ON188859	ON188936	ON189021
	CPCC 300310	Antarctica	Lichen	OM980443	OM980532	–	ON188981	ON188858	ON188934	–
	CPCC 300309	Antarctica	Lichen	OM980447	OM980536	–	ON188983	ON188860	ON188937	–
	CPCC 300308	Antarctica	Moss	OM980445	OM980534	–	ON188985	ON188862	ON188935	–
Piskurozyma viscida sp. nov.	CPCC 300400^{T}	Antarctica	Soil	OM980406	OM980495	ON007433	ON188961	ON188836	ON188897	–
	CPCC 300296	Antarctica	Lichen	OM980405	OM980494	ON007432	ON188960	ON188835	ON188896	–

Table 1. (Continued).

Species	Strain	Locality	Habitat	GenBank accession number						
				ITS	D1/D2	18S	*RPB1*	*RPB2*	*TEF1*	*CYTB*
Pricozyma crymophila sp. nov.	CPCC 300336^{T}	Arctic	Lichen	OM980389	OM980478	ON007420	ON188946	–	ON188883	–
	CPCC 300074	Antarctica	Lichen	OM980388	OM980477	–	–	–	–	–
	CPCC 300093	Antarctica	Lichen	OM980384	OM980473	–	ON188948	ON188827	ON188886	–
	CPCC 300311	Antarctica	Lichen	OM980385	OM980474	–	ON188950	–	ON188888	–
	CPCC 300312	Antarctica	Lichen	OM980387	OM980476	ON007422	ON188949	ON188828	ON188887	–
	CPCC 300054	Antarctica	Lichen	OM980386	OM980475	–	–	–	ON188885	–
	CPCC 300404	Arctic	Lichen	OM980390	OM980479	ON007421	ON188947	–	ON188884	–
Genolevuria ovata sp. nov.	CPCC 300327^{T}	Arctic	Vascular plant	OM980376	OM980465	ON007415	ON188942	ON188822	ON188878	–
	CPCC 300408	Arctic	Freshwater	OM980377	OM980466	ON007414	ON188941	ON188821	ON188877	–
Pseudotremella lichenophila sp. nov.	CPCC 300091^{T}	Antarctica	Lichen	OM980383	OM980472	ON007418	ON188944	ON188825	ON188881	–
	CPCC 300306	Antarctica	Lichen	OM980382	OM980471	ON007419	ON188945	ON188826	ON188882	–
Skadia corniformis sp. nov.	CPCC 300470^{T}	Arctic	Freshwater	OM980427	OM980516	ON007446	ON188973	–	ON188931	–
	CPCC 300506	Arctic	Freshwater	OM980425	OM980514	–	–	–	–	–
	CPCC 300509	Arctic	Freshwater	OM980424	OM980513	–	–	–	–	–
	CPCC 300515	Arctic	Freshwater	OM980426	OM980515	ON007447	–	ON188847	–	–
Skadia rubropurpurea sp. nov.	CPCC 300396^{T}	Arctic	Soil	OM980421	OM980510	ON007445	ON188972	ON188846	ON188930	–
	CPCC 300488	Arctic	Freshwater	OM980422	OM980511	ON007444	ON188971	–	ON188907	ON189012
	CPCC 300513	Arctic	Freshwater	OM980423	OM980512	–	–	–	–	–
Xiangyanghongia terricola sp. nov.	CPCC 300458^{T}	Antarctica	Soil	OM980380	OM980469	ON007417	ON188943	ON188824	ON188880	–
	CPCC 300456	Antarctica	Soil	OM980378	OM980467	–	–	–	–	–
	CPCC 300457	Antarctica	Soil	OM980379	OM980468	ON007416	–	ON188823	ON188879	–
	CPCC 300459	Antarctica	Soil	OM980381	OM980470	–	–	–	–	–
Xuelongia filamentosa sp. nov.	CPCC 300512^{T}	Arctic	Freshwater	OM980440	OM980529	ON007455	ON188977	ON188854	ON188913	ON189018
	CPCC 300450	Arctic	Freshwater	OM980441	OM980530	ON007457	ON188979	ON188856	ON188914	ON189020
	CPCC 300510	Arctic	Freshwater	OM980438	OM980527	–	–	–	–	–
	CPCC 300521	Arctic	Freshwater	OM980439	OM980528	–	–	–	–	–
Yunzhangia cylindrica sp. nov.	CPCC 300385^{T}	Arctic	Vascular plant	OM980417	OM980506	ON007441	ON188969	ON188844	ON188904	ON189009
	CPCC 300387	Arctic	Vascular plant	OM980418	OM980507	ON007440	ON188968	ON188843	ON188903	ON189008
	CPCC 300429	Arctic	Vascular plant	OM980416	OM980505	–	–	–	–	–
	CPCC 300491	Arctic	Vascular plant	OM980415	OM980504	–	–	–	–	–
	CPCC 300494	Arctic	Vascular plant	OM980414	OM980503	–	–	–	–	–
	CPCC 300495	Arctic	Vascular plant	OM980413	OM980502	–	–	–	–	–

D2 domains, 39 for 18S rDNA, 35 each for *RPB1* and *RPB2*, 36 for *TEF1*, and 21 for *CYTB* (Table 1). The sequence lengths for these loci in the seven-genes phylogeny of *Tremellomycetes* were: ITS 182 bp, D1/D2 domains 635 bp, 18S rDNA 1720 bp, *RPB1* 799 bp, *RPB2* 1077 bp, *TEF1* 982 bp, and *CYTB* 356 bp (Table S3). The sequence lengths for loci in the seven-genes phylogeny of *Microbotryomycetes* were: ITS 232 bp, D1/D2 domains 612 bp, 18S rDNA 1604 bp, *RPB1* 664 bp, *RPB2* 1065 bp, *TEF1* 947 bp, and *CYTB* 392 bp (Table S4). For the concatenated ITS-D1/D2 phylogeny analysis, sequences of closely related species and other phylogenetically important strains were retrieved from GenBank, as indicated in Tables S5, S6.

The analysis of the seven-gene phylogeny (Figs 3, 4) and the concatenated ITS-D1/D2 phylogeny (Figs S2–S7) identified 18 novel species among the 68 basidiomycetous yeast strains analysed, with nine species classified within *Tremellomycetes* and nine species within *Microbotryomycetes*. Thirteen of these novel species were classified within known genera, while five could not be integrated into existing classifications, resulting in the establishment of five new genera: *Chioneozyma*, *Pricozyma*, *Skadia*, *Xiangyanghongia*, and *Xuelongia*.

Novel taxa in *Tremellomycetes* (*Agaricomycotina*)

Pseudotremella (*Bulleraceae*, *Tremellales*)

Strains CPCC 300091 and CPCC 300306 exhibited identical sequences in the D1/D2 domains and differed by 1 nt mismatch in the ITS region, suggesting they belonged to the same species. In phylogenetic analyses, these strains formed a distinct clade within the genus *Pseudotremella*, as shown in the concatenated ITS-D1/D2 tree and seven-gene tree (Figs S2, 3). BLASTn analysis revealed that these two strains exhibited over 10 % mismatches (including substitutions and gaps) in the ITS region and 5 % mismatches in the D1/D2 domains with all known strains deposited in the GenBank. The closest undescribed yeast strains to CPCC 300091 and CPCC 300306 were *Tremella* sp. strain KBP:Y-6774 (GenBank MZ666407). These strains differed by 29 nt mismatches (24 nt substitutions and 5 nt gaps, 95.2 % identity and 100 % coverage) in the D1/D2 domains, and by 91–95 nt mismatches (55–56 nt substitutions and 35–39 nt gaps, 82.5–83.2 % identity and 90 % coverage) in the ITS region. The closest described species was *Pseudotremella rhododendri* CGMCC 2.6854^{T} (GenBank OP470282, OP470186), which differed by 95–96 nt mismatches (55–56 nt substitutions and 40 nt gaps, 82.7–82.9 % identity and 92 % coverage) in the ITS region and 34 nt mismatches (29 nt substitutions and 5 nt gaps, 94.1 % identity and 91–92 % coverage) in the D1/D2 domains. Based on these findings, a new species within *Pseudotremella* was proposed.

Genolevuria (*Bulleraceae*, *Tremellales*)

Strains CPCC 300327 and CPCC 300408 exhibited 1 nt substitution in the D1/D2 domains and shared identical ITS sequences, indicating that they were conspecific. In phylogenetic analyses, they clustered with *Genolevuria* sp. VKPM:Y-2726 and separated from all known species within *Genolevuria* in the concatenated ITS-D1/D2 tree (Fig. S2). They were also closely associated with the genus *Genolevuria* in the seven-gene phylogeny (Fig. 3), with strong support (bootstrap percentage = 100 %, posterior probability = 1.0). BLASTn analysis identified their closest relative as an uncharacterized strain, *Genolevuria* sp. strain VKPM:Y-2726 (GenBank OR004770), with which they differed by 7–8 nt substitutions in the D1/D2 domains (98.7–98.9 % identity, 100 % coverage) and 44 nt mismatches in the ITS region (33 nt substitutions and 11 nt gaps, 91.5–91.7 % identity, 88–90 % coverage). The closest described relative of CPCC 300327 and CPCC 300408 was *Genolevuria bromeliarum* CBS 10424^{T} (GenBank KY103461, DQ784566), differed by 43 nt mismatches in the D1/D2 domains (41 nt substitutions and 2 nt gaps, 92.8–92.9 % identity and 94–95 % coverage) and 74 nt mismatches in the ITS region (57 nt substitutions and 17 nt gaps, 84.4–84.7 % identity and 80–82 % coverage). Based on these findings, a novel species within the genus *Genolevuria* was established.

New family *Pricozymaceae* and novel genus *Pricozyma* (*Pricozymaceae, Tremellales*)

Seven strains – CPCC 300054, CPCC 300074, CPCC 300093, CPCC 300311, CPCC 300312, CPCC 300336, and CPCC 300404 – shared identical D1/D2 domain sequences and exhibited no more than 3 nt mismatches in the ITS regions, suggesting they were conspecific. In the seven-gene phylogenetic analysis (Fig. 3), this taxon clustered with *Naematelia aurantia* CBS 6965, *Dimennazyma cistialbidi* CBS 9931^{T}, and *Tremella indecorata* CBS 6976, members of the family *Naemateliaceae*. However, the node grouping *Naemateliaceae* with the new clade lacked bootstrap or posterior probability support. In the concatenated ITS-D1/D2 phylogenetic analysis (Fig. S2), they formed a distinct clade positioned between *Genolevuria* and *Tremella* Clade III, both within the family *Bulleraceae*, but this grouping also lacked support. The phylogenetic relationships suggested that the novel clade could not be assigned to either family. BLASTn results further revealed nucleotide divergences between the novel clade and its closely related relatives. The closest relative of the seven strains in the D1/D2 domains was *Genolevuria elizabethalexanderae* BRIP 71806a^{T} (GenBank OR271907, OR259048), differing by 34 nt substitutions (94.4–94.5 % identity and 98–100 % coverage). However, in the ITS region, it differed by 125–127 nt mismatches (65–67 nt substitutions and 60–62 nt gaps, 78.0–78.2 % identity and 99–100 % coverage). The closest relative of seven strains in the ITS region was *Fibulobasidium murrhardtense* CBS 9109^{T} (GenBank GU327540, AF416648), differing by 70 nt mismatches (44 nt substitutions and 26 nt gaps, 86.7–86.9 % identity and 99–100 % coverage). In the D1/D2 domains, it differed by 44 nt mismatches (43 nt substitutions and 1 nt gap, 91.9 % identity and 87–89 % coverage). Based on the phylogenetic analyses and BLASTn results, it is appropriate to propose a new family, *Pricozymaceae*, and a new genus, *Pricozyma*, for the new species.

Dioszegia (*Bulleribasidiaceae*, *Tremellales*)

Five strains formed two distinct clades within the genus *Dioszegia*. Strains CPCC 300431 and CPCC 300073 exhibited identical sequences in the D1/D2 domains, differing

by 4 nt substitutions in the ITS region, indicating they belonged to the same species. Similarly, strains CPCC 300379, CPCC 300401, and CPCC 300271 exhibited identical sequences in both the ITS region and D1/D2 domains, suggesting they were conspecific.

In the seven-gene and concatenated ITS-D1/D2 phylogenetic analyses, strains CPCC 300073 and CPCC 300431 clustered with *Dioszegia fristingensis* CBS 10052^T, *Dioszegia antarctica* CBS 10920^T, and *Dioszegia butyracea* CBS 10122^T, while strains CPCC 300271, CPCC 300379, and CPCC 300401 clustered with *Dioszegia xingshanensis* CBS 10120^T (Figs 3, S3). According to the BLASTn results, the closest relatives of CPCC 300073 and CPCC 300431 were *Dioszegia fristingensis* CBS 10052^T (GenBank AY562158, AY562146) and *Dioszegia antarctica* CBS 10920^T (GenBank DQ402529, FJ640575). Both strains shared identical D1/D2 domain sequences with their closest relatives but differed by 16 nt mismatches (10 nt substitutions and 6 nt gaps; 96.4 % identity and 88 % coverage) from *Dioszegia fristingensis* CBS 10052^T and by 25 nt mismatches (17 nt substitutions and 8 nt gaps; 94.5 % identity and 89 % coverage) from *Dioszegia antarctica* CBS 10920^T.

The closest relative of CPCC 300271, CPCC 300379, and CPCC 300401 was *Dioszegia xingshanensis* CBS 10120^T (GenBank EU070923, EU070928), which differed by 19 nt mismatches in the ITS region (13 nt substitutions and 6 nt gaps; 96.0–96.1 % identity and 92–94 % coverage) and 6 nt substitutions in the D1/D2 domains (99.0–99.1 % identity and 100 % coverage). In comparison, these three strains differed from *Dioszegia aurantiaca* CBS 6980^T (GenBank AB049613, AB104689) by 12 nt mismatches in the ITS region (5 nt substitutions and 7 nt gaps; 97.4 % identity and 89–93 % coverage), and 13 nt mismatches in the D1/D2 domains (12 substitutions and 1 gap; 97.8 % identity and 92–93 % coverage). Further analysis of the *TEF1* gene revealed that these three strains differed from *Dioszegia xingshanensis* CBS 10120^T (GenBank KF037139) by 76–78 nt mismatches (62–64 nt substitutions and 14 nt gaps; 88.2–88.5 % identity and 51 % coverage). Similarly, in the *TEF1* gene, these strains differed from *Dioszegia aurantiaca* CBS 6980^T (GenBank KF037131) by 70–72 nt mismatches (61–63 nt substitutions and 9 nt gaps; 88.9–89.2 % identity and 47 % coverage). Based on these findings, two novel species were proposed to accommodate these five strains.

Phaeotremella (*Phaeotremellaceae*, *Tremellales*)

Seven strains were identified within *Phaeotremella*, forming two distinct clades in both the seven-gene phylogeny (Fig. 3) and concatenated ITS-D1/D2 phylogeny (Fig. S4). Strains CPCC 300298, CPCC 300468, CPCC 300490, CPCC 300501, and CPCC 300516 differed from each other by no more than 4 nt mismatches in the D1/D2 domains and 3 nt mismatches in the ITS region, confirming their conspecific nature. Strains CPCC 300414 and CPCC 300496 exhibited identical sequences in both the D1/D2 domains and the ITS region, indicating they were also conspecific.

Strains CPCC 300298, CPCC 300468, CPCC 300490, CPCC 300501, and CPCC 300516 clustered closely with *Phaeotremella ovata* CGMCC 2.5614^T in both the seven-gene phylogeny (Fig. 3) and concatenated ITS-D1/D2 phylogeny (Fig. S4). The closest relatives to these five strains were *Phaeotremella ovata* CGMCC 2.5614^T (GenBank MK050281) and *Phaeotremella lactea* CGMCC 2.5810^T (GenBank MK050280). They differed from *Phaeotremella ovata* CGMCC 2.5614^T by 7–10 nt mismatches in the D1/D2 domains (5–6 nt substitutions and 2–5 nt gaps, 98.4–98.9 % identity and 100 % coverage) and 20–21 nt mismatches (16–17 nt substitutions and 4 nt gaps, 95.9–96.1 % identity and 100 % coverage) in the ITS region. Furthermore, they differed from *Phaeotremella lactea* CGMCC 2.5810^T by 5–9 nt mismatches in the D1/D2 domains (3–4 nt substitutions and 2–5 nt gaps, 98.5–99.2 % identity and 100 % coverage) and 21–23 nt mismatches in the ITS region (7–9 nt substitutions and 14 nt gaps, 93.7–94.1 % identity and 100 % coverage). Strains CPCC 300414 and CPCC 300496 clustered with *Phaeotremella camelliae* CGMCC 2.6141^T (GenBank MN450769) in both phylogenies (Figs 3, S4). They differed from *Phaeotremella camelliae* CGMCC 2.6141^T by 8 nt substitutions in the D1/D2 domains (98.7 % identity and 100 % coverage) and 28 nt mismatches in the ITS region (14 nt substitutions and 14 nt gaps, 93.9 % identity and 84–86 % coverage). Therefore, two new species were established to accommodate the identified clades within *Phaeotremella*.

New genus *Xiangyanghongia* (*Phaeotremellaceae*, *Tremellales*)

Strains CPCC 300456, CPCC 300457, CPCC 300458, and CPCC 300459 exhibited identical sequences in both the D1/D2 domains and the ITS region. They formed a separate clade in the concatenated ITS-D1/D2 phylogenetic tree (Fig. S4) but clustered with *Phaeotremella* in the seven-genes phylogeny with a rather long branch (Fig. 3), suggesting their distinct membership within *Phaeotremellaceae*. According to BLASTn results, the closest relative of these four strains among *Gelidatrema* species was *Gelidatrema psychrophila* JCM 32067^T (GenBank LC222847), differing by 30 nt mismatches in the D1/D2 domains (29 nt substitutions and 1 nt gap, 94.9 % identity and 94 % coverage) and by 67 nt mismatches in the ITS region (38 nt substitutions and 29 nt gaps, 86.7 % identity and 94 % coverage). Additionally, the closest relative of these four strains among *Phaeotremella* species was *Phaeotremella yunnanensis* voucher Dai 15660^T (GenBank MK559397, MK559399), differing by 56 nt mismatches in the ITS region (39 nt substitutions and 17 nt gaps, 86.9 % identity and 80 % coverage) and by 40 nt mismatches in the D1/D2 domains (28 nt substitutions and 12 nt gaps, 91.8 % identity and 97 % coverage). These nucleotide divergences also indicated that neither *Phaeotremella* nor *Gelidatrema* could accommodate the novel clade in the seven-genes and concatenated ITS-D1/D2 trees. Therefore, a new genus, *Xiangyanghongia*, and a new species of which was proposed.

Piskurozyma (*Piskurozymaceae*, *Filobasidiales*)

Strains CPCC 300296 and CPCC 300400 exhibited identical sequences in the D1/D2 domains and showed 2 nt mismatches in the ITS region, indicating that they were conspecific. In the seven-genes phylogenetic relationship, CPCC 300296 and CPCC 300400 clustered with *Piskurozyma linzhiensis* CGMCC 2.6919^T (GenBank OP470281, OP470285) and

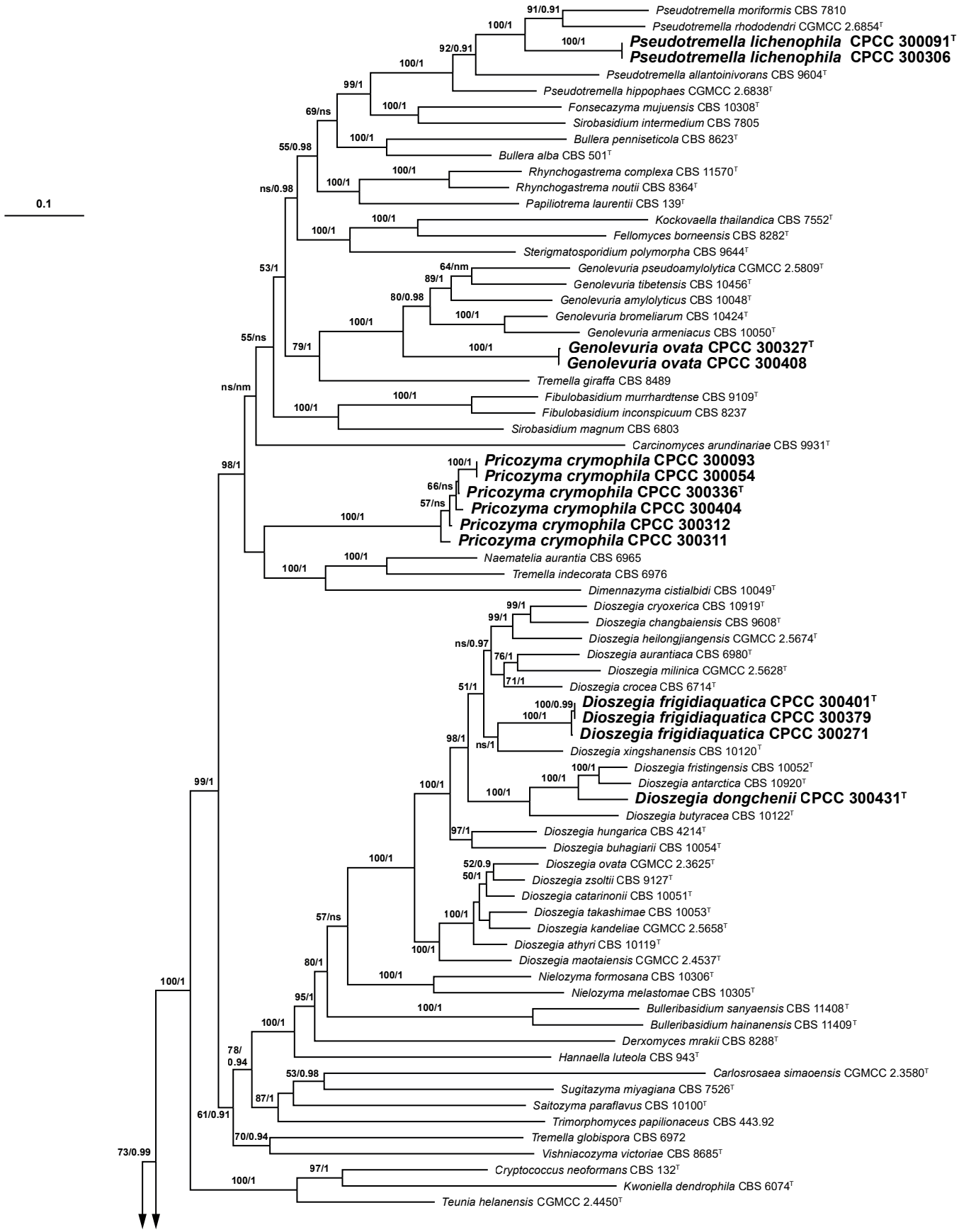

Fig. 3. Phylogenetic tree inferred using the combined sequences of ITS, D1/D2 domains, 18S rDNA, *RPB1*, *RPB2*, *TEF1*, and *CYTB*, showing the phylogenetic positions of new taxa (in **bold**) within *Tremellomycetes* (*Agaricomycotina*). The tree backbone was constructed using maximum likelihood analysis. Bootstrap percentages from maximum likelihood analysis (over 50 %) based on 1000 bootstrap replicates, and posterior probabilities of Bayesian inference (above 0.9), are shown respectively from left to right on deep and major branches. Scale bar = 0.1 substitutions per nucleotide position. Note: ns, not supported (BP < 50 % or PP < 0.9), nm, not monophyletic.

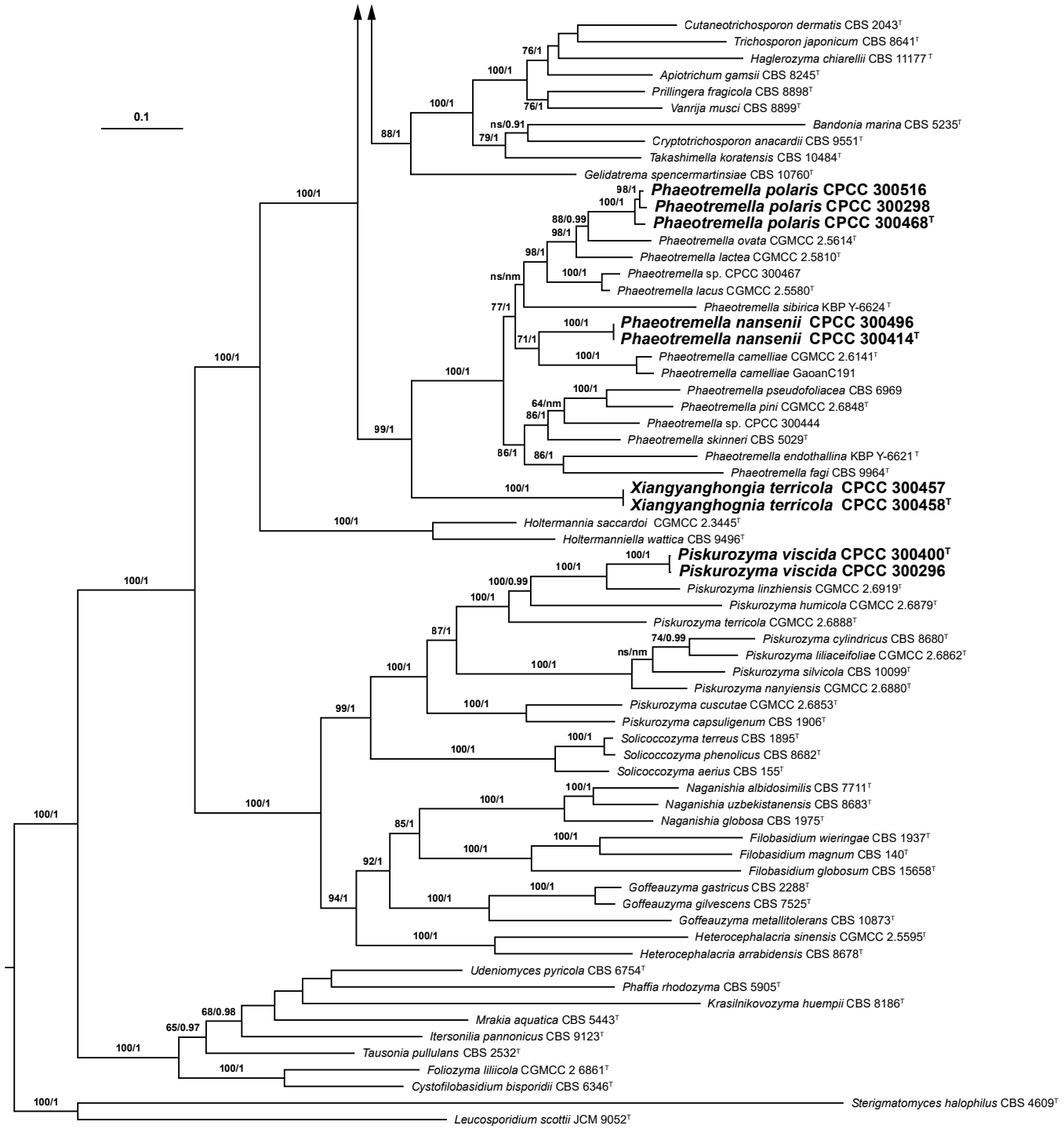

Fig. 3. Continued.

closely related to *Piskurozyma sorana* UBC F16310 (GenBank EU541305) in the concatenated ITS-D1/D2 tree (Figs 3, S5). According to BLASTn results, the closest relative of these two strains was *Piskurozyma linzhiensis* CGMCC 2.6919^T, differed by 22–24 nt mismatches in the ITS region (18–20 nt substitutions and 4 nt gaps,96.0–96.4 % identity and 91–92 % coverage) and 3 nt substitutions in the D1/D2 domains (99.5 % identity and 91 % coverage). Additionally, they differed from *Piskurozyma sorana* UBC F16310 by 69–70 nt mismatches in the ITS region (51–52 nt substitutions and 18 nt gaps, 87.2–87.5 % identity and 81–83 % coverage) and 22 nt mismatches in the D1/D2 domains (20 nt substitutions and 2 nt gaps, 96.1 % identity and 91 % coverage). Therefore, a new species of *Piskurozyma* was proposed.

Novel taxa in *Microbotryomycetes* (*Pucciniomycotina*)

New genera *Skadia and Xuelongia* (*Camptobasidiaceae*, *Incertae sedis*)

Many strains within the family *Camptobasidiaceae* were identified in the seven-gene phylogeny (Fig. 4) and concatenated ITS-D1/D2 phylogeny (Fig. S6). Strains CPCC 300396, CPCC 300488, and CPCC 300513 exhibited identical D1/D2 domains and differed by no more than 2 nt substitutions in the ITS region. Strains CPCC 300470, CPCC 300506, CPCC 300509, and CPCC 300515 exhibited identical sequences in both the ITS region and D1/D2 domains. Clade

CPCC 300396 and clade CPCC 300470 clustered together in both seven-gene and ITS-D1/D2 phylogeny analyses. These two clades were closely related to *Psychromyces* in the ITS-D1/D2 phylogeny. Furthermore, the above two clades were sister to another clade consisting of CPCC 300512, and CPCC 300450 in the seven-gene phylogeny (Fig. 4). Strains CPCC 300450, CPCC 300510, CPCC 300512, and CPCC 300521 exhibited identical sequences in the D1/D2 domains and showed no more than 1 nt mismatch in the ITS region. The concatenated ITS-D1/D2 phylogeny placed these four strains in a well-supported clade, which was phylogenetically distinct from *Cryolevonia*, *Glaciozyma,* and *Camptobasidium* (Fig. S6). Consequently, none of the known genera within *Camptobasidiaceae* (*Cryolevonia*, *Camptobasidium*, *Glaciozyma*, *Psychromyces*) could accommodate these clades, suggesting that they represent new genera within the family.

According to BLASTn results, the closest described relative of clade CPCC 300396 (strains CPCC 300396, CPCC 300488, and CPCC 300513) in the D1/D2 domains

Fig. 4. Phylogenetic tree inferred using the combined sequences of ITS, D1/D2 domains, 18S rDNA, *RPB1*, *RPB2*, *TEF1*, and *CYTB*, showing the phylogenetic positions of new taxa (in **bold**) within *Microbotryomycetes* (*Pucciniomycotina*). The tree backbone was constructed using maximum likelihood analysis. Bootstrap percentages from maximum likelihood analysis (over 50 %) from 1000 bootstrap replicates, and posterior probabilities of Bayesian inference (above 0.9), are shown respectively from left to right on deep and major branches. Scale bar = 0.1 substitutions per nucleotide position. Note: ns, not supported (BP < 50 % or PP < 0.9), nm, not monophyletic.

was *Phenoliferia psychrophenolica* CBS 10438^T (GenBank EF151246, KY108774), differing by 32 nt mismatches (31 nt substitutions and 1 nt gap, 94.8 % identity and 100 % coverage), and by 79–81 nt mismatches in the ITS region (53–55 nt substitutions and 26 nt gaps, 87.0–87.3 % identity and 96 % coverage). The closet relative of these three strains in the ITS region was *Camptobasidium hydrophilum* CCM 8060^T (GenBank MN626358, AY212991), differing by 38–39 nt mismatches (28–29 nt substitutions and 10 nt gaps, 91.9–92.1 % identity and 74 % coverage), and by 47 nt mismatches in the D1/D2 domains (30 nt substitutions and 17 nt gaps, 91.9 % identity and 94 % coverage). The closest described relative of clade CPCC 300470 (strains CPCC 300470, CPCC 300506, CPCC 300509, and CPCC 300515) in the D1/D2 domains was *Phenoliferia psychrophenolica* CBS 10438^T (GenBank EF151246, KY108774) as well, differing by 26 nt mismatches (23 nt substitutions and 3 nt gaps, 95.7 % identity and 100 % coverage), and by 88 nt mismatches in the ITS region (63 nt substitutions and 25 nt gaps, 85.8 % identity and 96 % coverage). The closest relative of these four strains in the ITS region was also *Camptobasidium hydrophilum* CCM 8060^T (GenBank MN626358, AY212991), differing by 38 nt mismatches (32 nt substitutions and 6 nt gaps, 92.0 % identity and 74 % coverage), and by 42 nt mismatches in the D1/D2 domains (25 nt substitutions and 17 nt gaps, 92.8 % identity and 94 % coverage). Additionally, clade CPCC 300396 and clade CPCC 300470 differed from each other by 22 nt substitutions (96.4 % identity and 99–100 % coverage) in the D1/D2 domains, and by 60–61 nt mismatches in the ITS region (49–50 nt substitutions and 11 nt gaps, 90.5–90.7 % identity and 99–100 % coverage). Therefore, a new genus, *Skadia*, was proposed for these two novel clades.

The closest described relative of strains CPCC 300450, CPCC 300510, CPCC 300512, and CPCC 300521 in the D1/D2 domains was *Camptobasidium gelus* CBS 8941^T (GenBank AY040665, AY040647), which differed by 16 nt substitutions (97.4 % identity and 100 % coverage). However, these strains showed 54 nt mismatches in the ITS region (26 nt substitutions and 28 nt gaps, 76–77 % coverage and 88.5–89.0 % identity). The closest relative of these four strains in the ITS region was *Psychromyces glacialis* CBS 16467^T (GenBank MK671633, MT301949), differing by 46 nt mismatches (19 nt substitutions and 27 nt gaps, 89.3 % identity and 67–69 % coverage), and 29 nt mismatches in the D1/D2 domains (24 nt substitutions and 5 nt gaps, 95.0 % identity and 95 % coverage). Therefore, a new genus, *Xuelongia*, was proposed for the new clade.

Glaciozyma (*Camptobasidiaceae*, *Incertae sedis*)

Two clades clustered with *Glaciozyma* in the seven-gene phylogeny (Fig. 4) and concatenated ITS-D1/D2 phylogeny (Fig. S6), supported by high bootstrap percentages and posterior probability. Strains CPCC 300077, CPCC 300449, CPCC 300511, CPCC 300492, and CPCC 300503 exhibited identical sequences in the D1/D2 domains and exhibited no more than 1 nt substitution in the ITS region, indicating they were conspecific. Strain CPCC 300395 shared identical sequences in both the ITS and D1/D2 domains with CPCC 300473, representing another conspecific clade. Clade CPCC 300077 differed from clade CPCC 300473 by 21–22 nt mismatches in the ITS region (9–10 nt substitutions and 12 nt gaps, 95.2–95.4 % identity, 88 % coverage), and by 7 nt mismatches in the D1/D2 domains (3 nt substitutions and 4 nt gaps, 98.8–98.9 % identity, 98–99 % coverage). Additional differences were observed with 43–46 nt mismatches in *RPB2* (43–45 nt substitutions and 0–1 nt gap, 95.8–96.0 % identity, 96–98 % coverage) and 30–31 nt substitutions in *TEF1* (96.7–97.0 % identity, 99–100 % coverage), indicating that they represent two distinct species. Clade CPCC 300077 differed from all known *Glaciozyma* species by ≥ 25

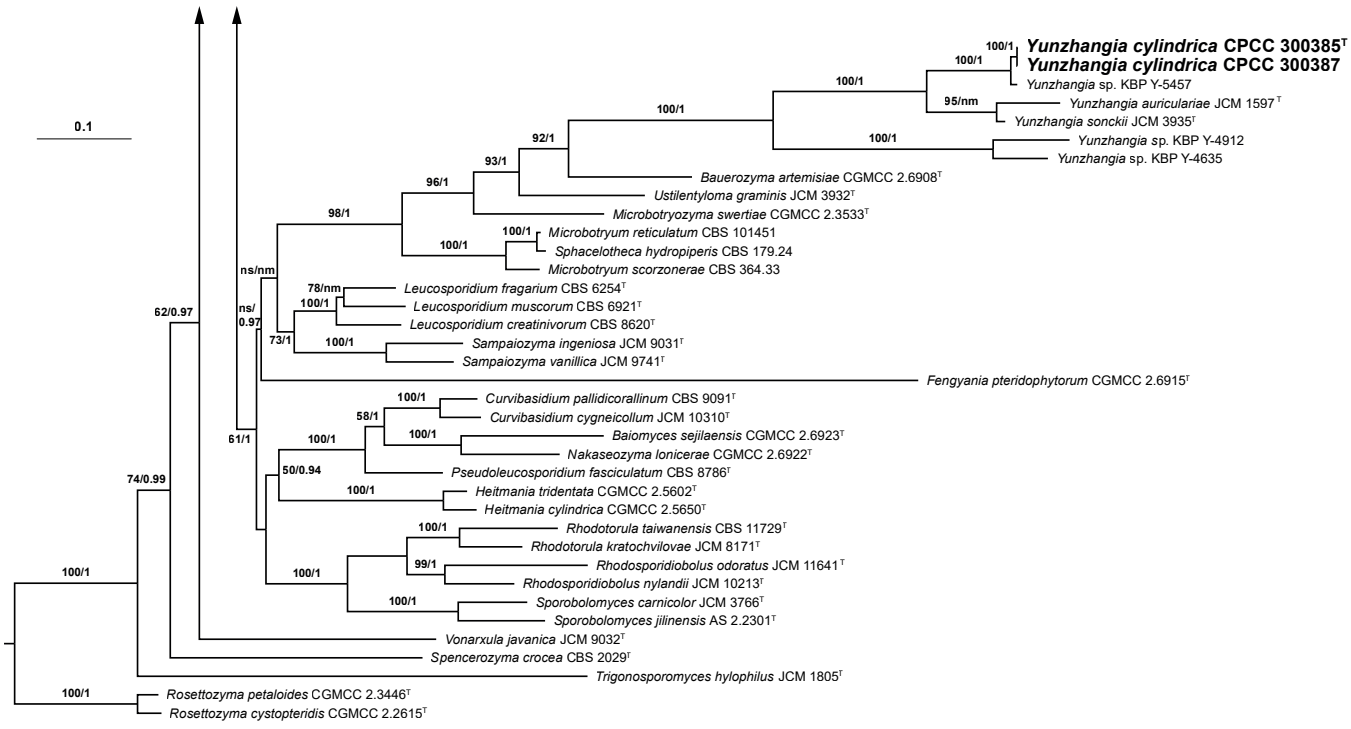

Fig. 4. Continued.

Table 2. Information on the 80 known yeast species isolated from various habitats in the Arctic and Antarctic regions identified in this study.

Yeast species	Arctic										Antarctica									Sum
	Soil	Freshwater	Seawater	Vascular plant	Moss	Lichen	Marine alga	Mushroom	Animal dung	Bird feather	Soil	Freshwater	Seawater	Vascular plant	Moss	Lichen	Green alga	Animal dung	Bird feather	
Ascomycota																				
Saccharomycetes																				
Saccharomycetales																				
Incertae sedis																				
Candida zeylanoides [S/N]	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1
'Candida davisiana' [S]	–	–	1	–	–	2	–	–	–	–	–	–	–	–	2	4	–	–	–	9
Candida glaebosa [S]	–	–	–	–	–	–	–	–	–	–	3	–	–	–	–	–	–	–	2	5
Candida railenensis [-]	–	–	–	–	–	–	–	–	–	–	–	1	2	–	–	–	–	–	–	3
Saccharomycetaceae																				
Debaryomyces hansenii [S/N]	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	1
Wickerhamomycetaceae																				
Wickerhamomyces anomalus [S/N]	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	1
Metschnikowiaceae																				
Metschnikowia australis [S]	–	–	–	–	–	–	–	–	–	–	–	–	82	–	–	–	–	–	–	82
M. bicuspidata [N]	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1
M. zobellii [N]	–	–	6	–	–	–	4	–	–	–	–	–	–	–	–	–	–	–	–	10
Basidiomycota																				
Agaricostilbomycetes																				
Agaricostilbales																				
Kondoaceae																				
Kondoa malvinella [S]	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	1
Cystobasidiomycetes																				
Cystobasidiales																				
Cystobasidiaceae																				
Cystobasidium laryngis [S/N]	1	1	6	4	1	1	–	–	9	–	10	4	3	–	3	2	2	1	1	49
C. ongulense [S/N]	1	–	–	–	–	1	–	–	–	–	11	4	6	–	1	2	–	1	–	27
C. psychroaquaticum [S/N]	–	1	1	–	4	–	–	–	2	1	–	–	–	–	–	–	–	–	–	9
C. raffinophilum [-]	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	1
Exobasidiomycetes																				
Exobasidiales																				

Table 2. (Continued).

Yeast species	Arctic										Antarctica									Sum
	Soil	Freshwater	Seawater	Vascular plant	Moss	Lichen	Marine alga	Mushroom	Animal dung	Bird feather	Soil	Freshwater	Seawater	Vascular plant	Moss	Lichen	Green alga	Animal dung	Bird feather	
Brachybasidiaceae																				
Meira plantarum [-]	–	–	–	–	–	–	–	–	–	–	–	2	–	–	–	–	–	–	–	2
Microbotryomycetes																				
Incertae sedis																				
Chrysozymaceae																				
Bannozyma arctica [S/N]	–	–	–	1	–	–	–	–	–	–	5	6	–	1	2	11	–	–	–	26
Kriegeriales																				
Camptobasidiaceae																				
Camptobasidium gelus [S/N]	3	11	2	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	16
Cryolevonia giraudoae [S]	–	15	–	–	–	–	–	–	–	–	17	3	–	–	–	–	–	–	–	35
C. schafbergensis [N]	1	17	–	–	–	–	–	–	–	–	3	–	–	–	–	–	–	–	–	21
Glaciozyma antarctica [S/N]	15	5	–	–	–	–	–	–	–	–	9	–	–	–	–	–	–	–	3	32
G. litoralis [S/N]	–	–	12	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	12
G. martinii [S]	4	2	–	–	–	–	–	–	–	–	14	–	1	–	–	1	–	1	–	23
G. watsonii [S/N]	16	12	–	–	–	–	–	–	1	–	15	1	–	–	–	–	–	–	–	45
Psychromyces glacialis[N]	–	–	–	–	–	–	–	–	–	–	2	–	–	–	–	–	–	–	–	2
Kriegeriaceae																				
Phenoliferia glacialis [S/N]	21	7	–	–	–	3	–	–	–	–	64	30	–	1	2	24	–	1	1	154
P. psychrophenolica [S/N]	9	30	4	1	–	5	–	–	–	–	10	22	–	1	1	10	–	–	–	93
P. psychrophila [S]	19	–	–	–	–	1	–	–	–	–	95	20	–	–	1	10	–	1	3	150
Curvibasidiales																				
Curvibasidiaceae																				
Curvibasidium nothofagi [-]	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	1
Heterogastridiales																				
Heterogastridiaceae																				
Slooffia velesii [-]	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	1
Leucosporidiales																				
Leucosporidiaceae																				
Leucosporidium creatinivorum [S/N]	–	–	–	–	–	–	–	–	–	–	–	1	–	–	1	7	2	–	–	11
L. fragarium [S/N]	–	–	–	–	–	–	–	–	–	–	3	–	–	–	1	–	–	8	–	12

Table 2. (Continued).

Yeast species	Arctic										Antarctica									Sum
	Soil	Freshwater	Seawater	Vascular plant	Moss	Lichen	Marine alga	Mushroom	Animal dung	Bird feather	Soil	Freshwater	Seawater	Vascular plant	Moss	Lichen	Green alga	Animal dung	Bird feather	
L. himalayensis [-]	–	–	–	–	–	–	–	–	–	–	5	–	–	1	–	–	–	2	–	8
L. muscorum [S/N]	7	11	4	1	–	–	–	–	–	1	20	17	–	–	–	1	–	–	–	62
L. scottii [S/N]	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1
L. yakuticum [S/N]	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	1
Sporidiobolales																				
Sporidiobolaceae																				
Rhodotorula taiwanensis [-]	–	–	–	–	–	–	–	–	–	–	–	–	3	–	–	–	–	–	–	3
Rhodotorula mucilaginosa [S/N]	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1
Rhodosporidiobolus oreadorum[N]	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1
Tremellomycetes																				
Cystofilobasidiales																				
Cystofilobasidiaceae																				
Cystofilobasidium macerans [S/N]	–	–	–	–	–	–	–	–	2	–	–	–	–	–	–	–	–	–	–	2
Mrakiaceae																				
Mrakia blollopis [S/N]	2	9	–	1	–	–	–	–	1	–	9	3	–	–	–	–	–	–	–	25
M. cryoconiti [N]	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1
M. frigida [S/N]	2	1	9	–	–	–	16	3	–	–	–	–	–	–	–	–	–	–	–	31
M. gelida [S/N]	34	3	–	43	–	5	3	–	4	1	2	3	–	1	1	3	13	5	2	123
M. hoshinonis [N]	–	–	–	–	–	–	–	–	–	1	–	–	1	–	–	–	–	–	–	2
M. niccombsii [S]	–	–	–	2	–	6	–	–	7	–	–	–	–	–	–	–	–	–	–	15
M. psychrophila [S/N]	2	–	–	–	–	1	–	–	–	–	11	4	–	3	5	62	3	–	1	92
M. robertii [S/N]	11	21	–	–	–	–	–	–	–	–	8	4	–	–	–	5	–	–	–	49
M. stelviica [-]	–	–	–	13	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	13
Tausonia pullulans [S/N]	–	–	–	–	1	3	–	–	–	–	–	–	–	–	–	–	–	–	–	4
Filobasidiales																				
Filobasidiaceae																				
Filobasidium magnum [S/N]	1	–	–	–	–	–	–	–	–	13	–	6	–	–	–	–	–	–	–	20
F. stepposum [S]	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1

Table 2. (Continued).

Yeast species	Arctic										Antarctica									Sum
	Soil	Freshwater	Seawater	Vascular plant	Moss	Lichen	Marine alga	Mushroom	Animal dung	Bird feather	Soil	Freshwater	Seawater	Vascular plant	Moss	Lichen	Green alga	Animal dung	Bird feather	
Goffeauzyma gastrica [S/N]	1	–	–	–	1	–	–	–	1	–	1	–	–	–	–	–	–	–	–	4
G. gilvescens [S/N]	7	28	32	–	11	2	–	4	38	2	17	5	–	–	1	–	–	–	2	149
Heterocephalacria sinensis [-]	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1
Naganishia adeliensis [S/N]	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	1
N. nivalis [-]	3	–	–	–	–	–	–	–	–	–	2	–	–	–	–	–	–	–	–	5
N. albidosimilis [S/N]	–	1	4	–	–	–	–	–	3	1	–	–	–	–	–	–	–	–	–	9
N. albida [S/N]	–	–	–	–	–	–	–	–	–	–	–	12	–	–	–	–	–	–	–	12
N. diffluens [S/N]	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1
N. globosa [S/N]	–	–	–	–	–	–	–	–	–	–	–	4	–	–	–	–	–	–	–	4
N. uzbekistanensis [-]	–	–	–	–	–	–	–	–	–	–	–	6	–	–	–	–	–	–	–	6
N. vaughanmartiniae [S/N]	–	–	7	–	–	–	–	–	–	–	2	–	–	–	–	–	–	–	–	9
Piskurozymaceae																				
Piskurozyma fildesensis [S/N]	2	–	–	–	–	2	–	–	–	–	–	–	–	–	–	13	–	–	–	17
P. yama [-]	2	–	–	3	–	–	–	–	–	–	1	–	–	–	1	–	–	–	–	7
Solicoccozyma terricola [S/N]	1	–	–	–	–	–	–	–	–	–	–	–	–	–	1	8	–	–	–	10
Holtermanniales																				
Holtermanniaceae																				
Holtermanniella festucosa [S/N]	–	–	33	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	34
H. nyarrowii [S]	–	1	–	–	–	–	–	–	–	–	–	2	–	–	–	2	–	–	–	5
H. wattica [S/N]	–	–	–	–	–	–	–	–	–	–	1	1	–	–	–	–	–	4	–	6
Tremellales																				
Phaeotremellaceae																				
Gelidatrema psychrophila [N]	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1
Phaeotremella lacus [-]	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1
Cryptococcaceae																				
Kwoniella ovata [-]	–	–	–	–	–	–	–	–	–	–	–	16	–	–	–	–	–	–	–	16
Tremellaceae																				
Tremella indecorata [S]	–	–	–	–	–	5	–	–	–	–	–	–	–	–	–	–	–	–	–	5

Table 2. (Continued).

Yeast species	Arctic										Antarctica									Sum
	Soil	Freshwater	Seawater	Vascular plant	Moss	Lichen	Marine alga	Mushroom	Animal dung	Bird feather	Soil	Freshwater	Seawater	Vascular plant	Moss	Lichen	Green alga	Animal dung	Bird feather	
Bulleribasidiaceae																				
Dioszegia antarctica [S]	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1
Dioszegia crocea [S/N]	–	–	–	–	–	–	–	–	–	–	–	–	–	2	–	–	–	–	–	2
D. rishiriensis [-]	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1
D. hungarica [S/N]	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	1
Vishniacozyma carnescens [S/N]	–	3	1	–	–	–	–	–	–	–	1	–	27	–	–	–	–	–	–	32
V. foliicola [S]	–	–	–	–	–	–	–	–	–	–	–	–	4	–	–	–	–	–	–	4
V. tephrensis [S/N]	16	4	4	12	–	4	–	–	1	1	–	–	4	–	–	–	–	–	–	46
V. victoriae [S/N]	8	43	48	150	–	12	3	–	10	31	12	32	50	9	23	9	12	8	9	469
Number of samples	43	45	24	54	17	18	4	3	13	13	48	20	18	6	15	46	5	7	7	406
Number of isolates	190	231	176	236	18	53	27	7	80	52	355	211	184	19	47	176	32	32	24	2 150
Number of species	26	26	18	16	5	15	5	2	13	9	30	27	12	8	16	19	5	10	9	80

The suffix [N] refers to species has been previously isolated from the Arctic regions.

The suffix [S] refers to species has been previously isolated from the Antarctic regions.

The suffix [S/N] refers to species has been previously isolated both from the Arctic and Antarctic regions.

The suffix [-] refers to species has never been isolated from the Arctic and Antarctic regions.

nt substitutions (≤ 92.4 % identity) in the ITS region and ≥ 13 nt substitutions (≤ 97.0 % identity) in the D1/D2 domains. Similarly, clade CPCC 300473 differed by ≥ 25 nt substitutions (≤ 90.7 % identity) in the ITS region and ≥16 nt substitutions (≤ 95.9 % identity) in the D1/D2 domains. Therefore, two new *Glaciozyma* species were proposed.

New genus *Chioneozyma* (*Kriegeriaceae*, *Kriegeriales*)

In the seven-gene phylogenetic analysis (Fig. 4), the seven strains formed two well-supported clades within the family *Kriegeriaceae*, which was phylogenetically distinct from the *Phenoliferia* species (Fig. 4). In the concatenated ITS-D1/D2 phylogeny (Fig. S6), these strains formed a cluster with *Phenoliferia*, but this association was weakly supported (bootstrap ≤ 50 %). These phylogenetic analyses supported the recognition of these strains as a distinct evolutionary lineage within the family *Kriegeriaceae*. Clade CPCC 300339, consisting of five strains (CPCC 300081, CPCC 300302, CPCC 300339, CPCC 300493, and CPCC 300500), exhibited identical sequences in the D1/D2 domains. Strain CPCC 300339 differed from the other four strains by 1 nt mismatch in the ITS region. In contrast, clade CPCC 300299, consisting of four strains (CPCC 300299, CPCC 300308, CPCC 300309, and CPCC 300310), exhibited identical sequences in both the D1/D2 domains and the ITS region. According to BLASTn results, these nine strains differed from *Phenoliferia psychrophenolica* CBS 10438^T (GenBank EF151246, KY108774) by 9 nt substitutions in the D1/D2 domains (98.5 % identity, 100 % coverage) and 34–37 nt mismatches in the ITS region (16–19 nt substitutions and 18 nt gaps, 93.8–94.4 % identity, 95–96 % coverage). They differed from *Phenoliferia psychrophila* CBS 10440^T (GenBank KY104504, KY108775) by 11 nt substitutions in the D1/D2 domains (98.2 % identity, 100 % coverage) and 22–23 nt mismatches in the ITS region (10–14 nt substitutions and 8–13 nt gaps, 96.2–96.5 % identity, 97 % coverage). They differed from *Phenoliferia glacialis* CBS 10436^T (GenBank KY104503, KY108773) by 14 nt substitutions in the D1/D2 domains (97.7 % identity and 100 % coverage) and 22–23 nt mismatches in the ITS region (96.2–96.4 % identity and 97–98 % coverage). In all nine strains, the D1/D2 domain sequences were identical, with no more than 5 nt mismatches observed in the ITS region. However, comparisons of *RPB1*, *RPB2*, and *TEF1* sequences revealed significant divergences between the two clades, indicating they represent two distinct species. Clade CPCC 300299 differed from clade CPCC 300339 by 94 nt mismatches in *RPB1* (92 nt substitutions and 2 nt gaps, 85.9–86.0 % identity, 99–100 % coverage), 123 nt mismatches in *RPB2* (121 nt substitutions and 2 nt gaps, 88.8 % identity, 100 % coverage), and 31–45 nt mismatches in *TEF1* (25–39 nt substitutions and 6 nt gaps, 95.3–96.8 % identity, 98–100 % coverage). Based on these analyses, a new genus, *Chioneozyma*, and two new species were proposed.

Yunzhangia (*Incertae sedis, Incertae sedis*)

Strains CPCC 300385, CPCC 300387, CPCC 300429, CPCC 300491, CPCC 300494, and CPCC 300495 exhibited identical sequences in the D1/D2 domains and showed no more than 1 nt mismatch in the ITS region, indicating they were conspecific. These strains, along with an undescribed strain *Yunzhangia* sp. KBP:Y-5457, formed a cluster with *Yunzhangia sonckii* JCM 3935^T in the concatenated ITS-D1/D2 phylogeny (Fig. S7). In the seven-gene phylogeny (Fig 4), the clade containing CPCC 300385 and *Yunzhangia* sp. KBP:Y-5457 clustered with the two known *Yunzhangia* species. These strains differed from *Yunzhangia sonckii*

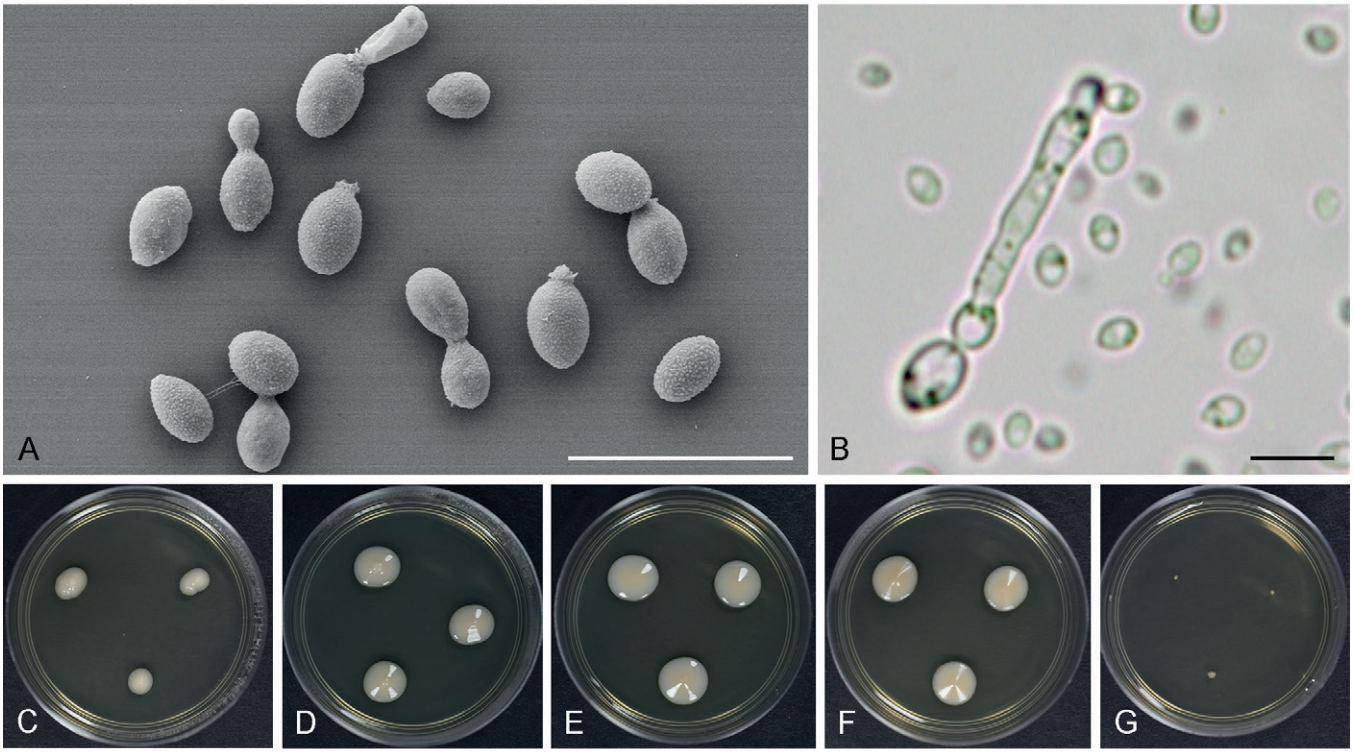

Fig. 5. *Pseudotremella lichenophila*. **A.** SEM image of vegetative cells grown in YM broth after 4 d at 12 °C (CPCC 300091^T). **B.** Light microscopy image of vegetative cells and hyphae grown on YM agar after 7 d at 15 °C (CPCC 300306). **C–G.** Views of colonies on YM agar at 4, 10, 15, 20, and 25 °C after 4 wk (CPCC 300091^T). Scale bars = 10 µm.

JCM 3935^T (GenBank AF444601, AF189969) by 28 nt mismatches in the D1/D2 domains (23 nt substitutions and 5 gaps, 95.4–95.5 % identity, 100 % coverage) and by 86–87 nt mismatches in the ITS region (46–47 nt substitutions and 40 nt gaps, 84.7–85.2 % identity, 95 % coverage). Based on these results, a new *Yunzhangia* species was proposed.

Fellozyma (*Chrysozymaceae, Incertae sedis*)

Three strains, CPCC 300300, CPCC 300301, and CPCC 300418, shared identical genetic sequences in the D1/D2 domains and exhibited no more than 2 nt mismatches in the ITS region, indicating they were conspecific. These three strains were found to cluster closely with *Fellozyma inositophila* JCM 5653^T in both the seven-gene phylogeny (Fig. 4) and the concatenated ITS-D1/D2 phylogeny (Fig. S6). These three strains differed from *Fellozyma inositophila* CBS 7310^T = JCM 5654^T (GenBank AF444559, AF189987) by 1 nt substitution in the D1/D2 domains (99.8 % identity and 100 % coverage) and 37–39 nt mismatches (14 nt substitutions and 23–25 nt gaps, 93.9–94.2 % identity and 96 % coverage) in the ITS region. They also differed from *Fellozyma pinalis* VKM Y-2963^T (GenBank OM666053) by 3 nt substitutions in the D1/D2 domains (99.5 % identity and 100 % coverage) and 12 nt mismatches in the ITS region (7 nt substitutions and 5 nt gaps, 98.0 % identity and 92 % coverage). Furthermore, these three strains differed from *Fellozyma inositophila* JCM 5654^T (GenBank KJ708136, KJ708306) by 143 nt mismatches in *RPB1* (121 nt substitutions and 21 nt gaps, 79.4 % identity and 100 % coverage) and 94–107 nt mismatches in *RPB2* (87–100 nt substitutions and 7 nt gaps, 85.1–85.5 % identity and 66–73 % coverage). Therefore, a new *Fellozyma* species was proposed.

Novel species descriptions

New taxa in *Tremellomycetes* (*Agaricomycotina*)

Pseudotremella lichenophila J.J. Feng & T. Zhang, ***sp. nov.*** MB 843888. Fig. 5.

Etymology: The specific epithet *lichenophila* refers to the substrate from which the ex-type strain was isolated.

Culture characteristics: After 7 d in YM broth at 15 °C, a sediment is formed. After 28 d in YM broth at 15 °C, a sediment and a ring (sometimes weak) can be observed. After 7 d on YM agar at 15 °C, cells are globose or ellipsoid to ovoid, 4.9–6.4 × 3.3–4.8 µm in size, occurring mainly single or in pairs, occasionally in triple, budding is polar. Sometimes elongate hyphae germinated from two conjugated vegetative yeast cells can be observed, clavate, about 26 µm in length and 5 µm in width. After 28 d on YM agar at 15 °C, the colonies are cream to white or yellowish white, butyrous, smooth, and flat. The margin is entire. Pseudohyphae cannot be observed in the Dalmau plate culture on CMA at 15 °C. Sexual reproduction cannot be observed on CMA, MEA, PDA, SYA, or YM agar.

Physiological characteristics: All the following assimilation and related tests were conducted at 15 °C. Fermentation is negative. The following sole carbon compounds can be assimilated: Glucose, melibiose (weak), galactose, sucrose (variable), lactose (delayed and weak), melezitose (weak), trehalose (sometimes delayed), salicin (variable), L-arabinose, L-rhamnose (weak), galactitol (delayed or weak), N-acetyl-D-glucosamine, D-mannitol, cellobiose (delayed),

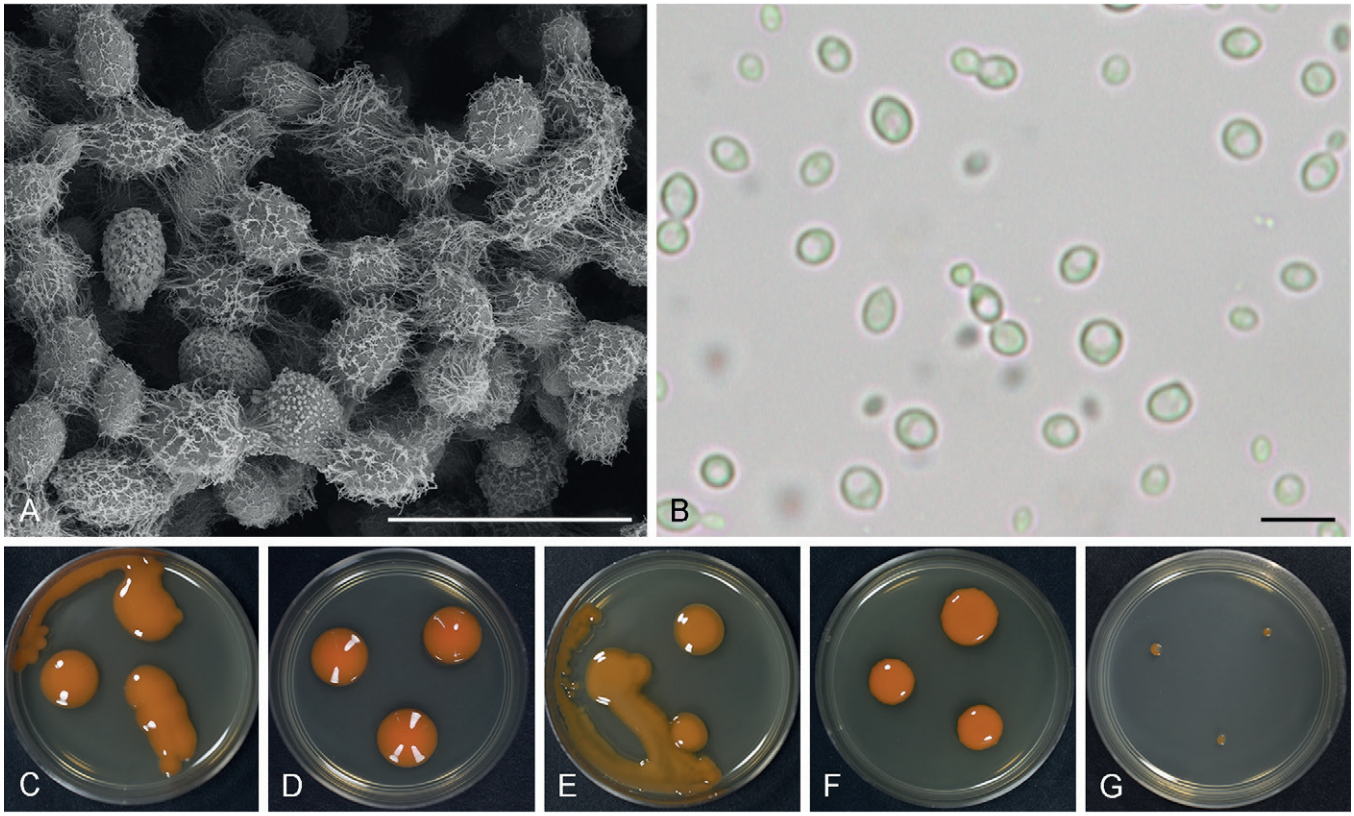

Fig. 6. *Genolevuria ovata* CPCC 300327^T. **A.** SEM image of vegetative cells grown in YM broth after 6 d at 12 °C. **B.** Light microscopy image of vegetative cells grown on YM agar after 7 d at 15 °C. **C–G.** Views of colonies on YM agar at 4, 10, 15, 20, and 25 °C after 4 wk. Scale bars = 10 µm.

raffinose (weak or delayed and weak), D-xylose, myo-inositol (delayed or weak), D-arabinose (delayed or weak), L-sorbose (weak or delayed and weak), inulin (variable), D-ribose (delayed), D-glucosamine, D-glucitol (sometimes delayed), glycerol (weak), ethanol (delayed or weak), D-Glucono-1,5-lactone, succinate, DL- lactate (weak or delayed and weak), D-gluconate, ribitol, maltose (sometimes weak), citrate, soluble starch (weak), xylitol (sometimes delayed), D-galacturonate, arbutin (variable), DL-malic acid (delayed and weak), L-arabinitol (sometimes delayed), D-glucuronate. The following sole carbon compounds cannot be assimilated: Methyl-α-D-glucoside, methanol, hexadecane, erythritol, levulinic acid, butane-2,3-diol, isopropanol, propane-1,2-diol. The following sole nitrogen compounds can be assimilated: Ammonium sulphate, L-lysine, ethylamine hydrochloride (sometimes delayed), cadaverine dihydrochloride, potassium nitrate. The following sole nitrogen compound cannot be assimilated: Sodium nitrite. Growth in vitamin-free medium is delayed. Growth is negative at 25 °C. Optimal growth temperature is between 10 °C and 20 °C. Growth in 0.01 % cycloheximide (w/v) is delayed or positive, while growth in 0.1 % cycloheximide (w/v) is negative. Growth on 10 % NaCl + 5 % glucose medium (w/v) and 50 % glucose agar (w/w) are negative. Extracellular starch-like compounds are not produced. Urease reaction is positive. Diazonium Blue B reaction is positive.

Typus: **Antarctica**, King George Island, Fildes Region, obtained from lichen, Jan. 2017, *T. Zhang* (**holotype** CPCC 300091^{T} preserved in a metabolically inactive state, culture ex-type CBS 18345 = PSL15).

Genolevuria ovata T. Zhang & J.J. Feng, ***sp. nov.*** MB 858794. Fig. 6.

Etymology: The scientific epithet *ovata* refers to the ovoid morphology of the yeast cells under microscopic observation.

Culture characteristics: After 7 d in YM broth at 15 °C, a sediment is formed. After 28 d in YM broth at 15 °C, a sediment and a very weak ring can be observed. After 7 d on YM agar at 15 °C, cells are subglobose to ovoid, 4.8–7.3 × 4.0–5.7 µm in size, occurring mainly single or in pairs, sometimes in triple or in a chain that consists of three cells, budding is polar. After 28 d on YM agar at 15 °C, the colonies are carroty to orange, mucoid, smooth, flat, and glistening. The margin is entire. Pseudohyphae or true hyphae cannot be observed in the Dalmau plate culture on CMA at 15 °C. Sexual reproduction cannot be observed on CMA, MEA, PDA, SYA, or YM agar.

Physiological characteristics: All the following assimilation and related tests were conducted at 15 °C. Fermentation is negative. The following sole carbon compounds can be assimilated: Glucose, melibiose, galactose, sucrose (weak), lactose, trehalose, salicin (delayed), L-arabinose, L-rhamnose (weak), galactitol, N-acetyl-D-glucosamine (weak), D-mannitol, cellobiose (delayed), raffinose, D-xylose, myo-inositol (delayed), D-arabinose (weak), inulin (weak), D-ribose (weak), D-glucosamine (delayed), D-glucitol, D-Glucono-1,5-lactone (weak), D-gluconate (weak), ribitol, maltose (weak), xylitol (weak), D-galacturonate (weak), arbutin (weak), DL-malic acid (weak), L-arabinitol (weak), D-glucuronate (weak). The following sole carbon compounds cannot be assimilated: Melezitose, methyl-α-D-glucoside, L-sorbose, glycerol, ethanol, methanol, succinate, DL-lactate, hexadecane, erythritol, citrate, soluble starch, levulinic acid, butane-2,3-diol, isopropanol, propane-1,2-diol. The following sole nitrogen compounds can be assimilated: Ammonium sulphate, L-lysine (delayed), cadaverine dihydrochloride (delayed), potassium nitrate (delayed). The following sole nitrogen compounds cannot be assimilated: Ethylamine hydrochloride, sodium nitrite. Growth in vitamin-free medium is weak. Growth is negative or weak at 25 °C, but negative at 28 °C. Optimal growth temperature is between 4 °C and 15 °C. Growth in 0.01 % cycloheximide (w/v) is delayed and weak, while growth in 0.1 % cycloheximide (w/v) is negative. Growth on 10 % NaCl + 5 % glucose medium (w/v) and 50 % glucose agar (w/w) are negative. Extracellular starch-like compounds are not produced. Urease reaction is positive. Diazonium Blue B reaction is positive.

Typus: **Spitsbergen** (Svalbard archipelago), Ny-Ålesund, obtained from vascular plant, Jul. 2019, *T. Zhang* (**holotype** CPCC 300327^{T} preserved in a metabolically inactive state, culture ex-type CBS 18344 = ZT33).

Note: Physiologically, *Genolevuria ovata* differed from all the other species within *Genolevuria* with available physiological characteristics in the inability to assimilate melezitose (Inácio *et al.* 2005, Wang *et al.* 2007, Landell *et al.* 2009, Li *et al.* 2020).

Pricozymaceae T. Zhang & J.J. Feng, ***fam. nov.*** MB 843952.

Member of the *Tremellales* (*Tremellomycetes*). The diagnosis of the family *Pricozymaceae* is based on the genus *Pricozyma*. The nomenclature of the family is based on the genus *Pricozyma*.

Type genus: *Pricozyma* T. Zhang & J.J. Feng

Pricozyma T. Zhang & J.J. Feng, ***gen. nov.*** MB 843953.

Etymology: The genus name refers to the Polar Research Institute of China and PRIC is the abbreviation of the organization.

This genus is proposed for the clade represented by CPCC 300054, CPCC 300074, CPCC 300093, CPCC 300311, CPCC 300312, CPCC 300336, and CPCC 300404. Member of *Tremellales.* The genus is mainly circumscribed by the seven-genes phylogenetic relationship, in which it occurred as a separate branch within the *Tremellales*.

Sexual reproduction not known. Colonies cream to yellowish white, butyrous. Budding cells present. Fermentation is negative. Cells are mainly ovoid to ellipsoidal. Pseudohyphae are not produced but hyphae can be observed in some strains of *Pricozyma crymophila*.

Type species: *Pricozyma crymophila* T. Zhang & J.J. Feng

Pricozyma crymophila T. Zhang & J.J. Feng, ***sp. nov.*** MB 843954. Fig. 7.

Etymology: The scientific epithet *crymophila* refers to the cold-adapted or cold-resistant profile of the species.

Culture characteristics: After 7 d in YM broth at 15 °C, a sediment is formed. After 28 d in YM broth at 15 °C, a sediment and a weak ring (sometimes partial) can be formed or not. After 7 d on YM agar at 15 °C, cells are subglobose to ovoid or ellipsoidal, 4.4–7.4 × 3.4–4.9 µm in size, occurring

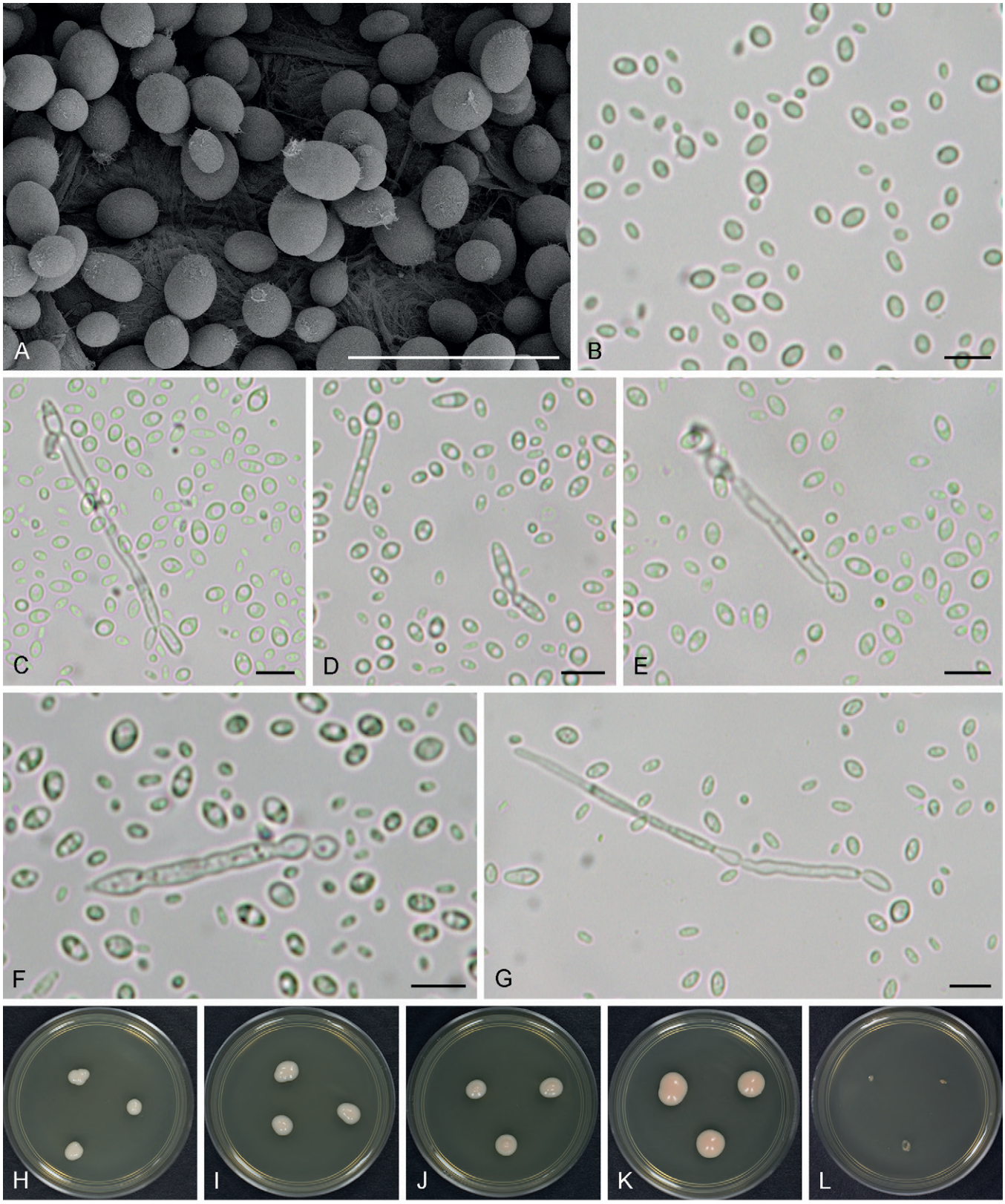

Fig. 7. *Pricozyma crymophila*. **A.** SEM image of vegetative cells grown in YM broth after 6 d at 12 °C (CPCC 300336^{T}). **B.** Light microscopic image of vegetative cells grown on YM agar after 7 d at 15 °C (CPCC 300336^{T}). **C**–**G.** Septate or aseptate hyphae grown on various agar media after 3 wk at 15 °C (**C,D.** CPCC 300054 on YM agar, **E.** CPCC 300093 on SYA, **F.** CPCC 300093 on PDA, **G.** CPCC 300074 on CMA). **H**–**L.** Views of colonies on YM agar at 4, 10, 15, 20, and 25 °C after 4 wk (CPCC 300336^{T}). Scale bars = 10 µm.

single or in pairs, budding is polar. After 28 d on YM agar at 15 °C, the streak culture is cream to yellowish white, butyrous, smooth, and flat. The margin is entire. Pseudohyphae or true hyphae cannot be observed in the Dalmau plate culture on CMA at 15 °C. Sexual reproduction cannot be observed on CMA, MEA, PDA, SYA, or YM agar. Additionally, septate or aseptate hyphae derived from individual or conjugated vegetative yeast cells can be observed in strain CPCC 300054, CPCC 300074, and CPCC 300093 on CMA, SYA, PDA, and YM agar after 3 wk at 15 °C.

Physiological characteristics: All the following assimilation and related tests were conducted at 15 °C. Fermentation is negative. The following sole carbon compounds can be assimilated: Glucose, melibiose (sometimes delayed or weak), galactose (sometimes delayed or delayed and weak), sucrose (variable), lactose (sometimes delayed or weak), melezitose (variable), trehalose (variable), salicin (delayed or delayed and weak or weak), L-arabinose (sometimes delayed or delayed and weak), L-rhamnose (variable), galactitol (variable), N-acetyl-D-glucosamine (sometimes delayed or delayed and weak or weak), methyl-α-D-glucoside (variable), D-mannitol (variable), cellobiose (sometimes delayed or delayed and weak), raffinose (delayed and weak or weak), D-xylose (delayed and weak), D-arabinose (sometimes delayed and weak), L-sorbose (variable), inulin (variable), D-ribose (delayed or delayed and weak or weak), D-glucosamine (sometimes delayed or delayed and weak), D-glucitol (sometimes delayed or delayed and weak), glycerol (variable), ethanol (variable), D-Glucono-1,5-lactone (sometimes delayed or weak), succinate (delayed or delayed and weak or weak), DL-lactate (variable), D-gluconate (sometimes delayed or weak), erythritol (variable), ribitol (sometimes delayed), maltose (variable), citrate (delayed or delayed and weak), soluble starch (variable), xylitol (sometimes delayed or weak), D-galacturonate (delayed or weak), arbutin (delayed and weak), DL-malic acid (variable), L-arabinitol (sometimes delayed or weak), D-glucuronate (sometimes delayed or delayed and weak or weak). The following sole carbon compounds cannot be assimilated: Myo-inositol, methanol, hexadecane, levulinic acid, butane-2,3-diol, isopropanol, propane-1,2-diol. The following sole nitrogen compounds can be assimilated: Ammonium sulphate (sometimes delayed), L-lysine (sometimes delayed), ethylamine hydrochloride (variable), cadaverine dihydrochloride (sometimes delayed), potassium nitrate (sometimes delayed). The following sole nitrogen compound cannot be assimilated: Sodium nitrite. Growth in vitamin-free medium is delayed or delayed and weak. Growth is negative or weak at 25 °C, but negative at 28 °C. Optimal growth temperature is between 10°C and 20 °C. Growth in 0.01 % cycloheximide (w/v) is negative. Growth on 10 % NaCl + 5 % glucose medium (w/v) and 50 % glucose agar (w/w) are negative. Extracellular starch-like compounds are not produced. Urease reaction is positive. Diazonium Blue B reaction is positive.

Typus: **Spitsbergen** (Svalbard archipelago), Ny-Ålesund, obtained from lichen, Jul. 2018, *T. Zhang* (**holotype** CPCC 300336^{T} preserved in a metabolically inactive state, culture ex-type CBS 18343 = ZT98).

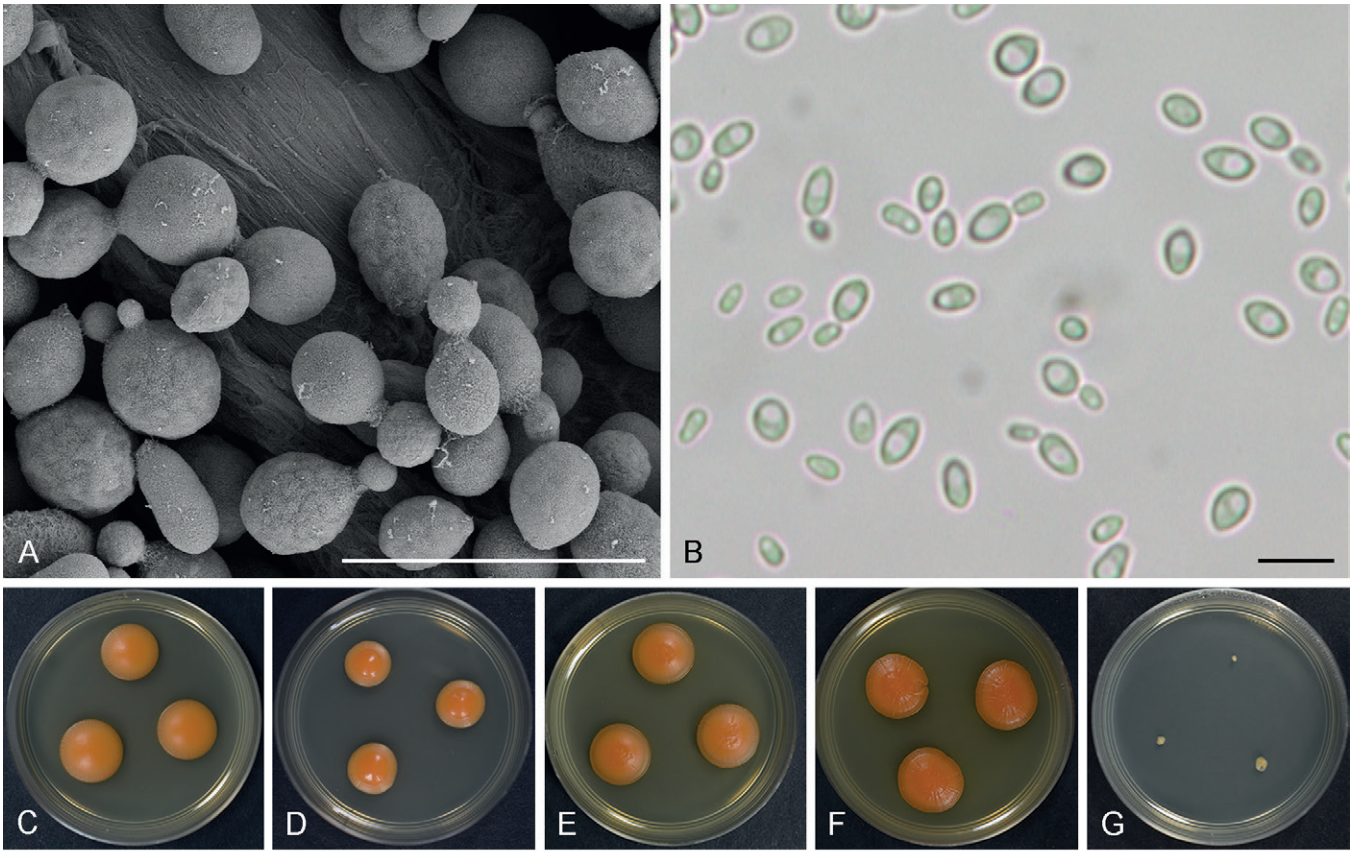

Fig. 8. *Dioszegia frigidiaquatica* CPCC 300401^{T}. **A.** SEM image of vegetative cells grown in YM broth after 6 d at 12 °C. **B.** Light microscopy image of vegetative cells grown on YM agar after 7 d at 15 °C. **C**–**G.** Views of colonies on YM agar at 4, 10, 15, 20, and 25 °C after 4 wk. Scale bars = 10 µm.

Dioszegia frigidiaquatica T. Zhang & J.J. Feng, ***sp. nov.*** MB 843895. Fig. 8.

Etymology: The scientific epithet *frigidiaquatica* refers to cold water, the characteristic and the substrate from which the species was first described.

Culture characteristics: After 7 d in YM broth at 15 °C, a sediment and a ring (sometimes weak) are formed. After 28 d in YM broth at 15 °C, a sediment and a ring can be observed, pellicle can or cannot be observed. After 7 d on YM agar at 15 °C, cells are subglobose to ellipsoidal, 5.6–8.1 × 4.0–5.4 µm in size, occurring mainly single or in pairs, sometimes in triple or in a chain that consists of three to four cells, budding is polar. After 28 d on YM agar at 15 °C, the colonies are carroty to orange or light orange, butyrous, smooth, and flat. The margin is entire. Pseudohyphae or true hyphae cannot be observed in the Dalmau plate culture on CMA at 15 °C. Sexual reproduction cannot be observed on CMA, MEA, PDA, SYA, or YM agar.

Physiological characteristics: All the following assimilation and related tests were conducted at 15 °C. Fermentation is negative. The following sole carbon compounds can be assimilated: Glucose, melibiose, galactose, sucrose, melezitose, trehalose, salicin, L-arabinose, L-rhamnose (variable), galactitol, N-acetyl-D-glucosamine, methyl-α-D-glucoside, D-mannitol, cellobiose (sometimes delayed), raffinose, D-xylose, myo-inositol (delayed or weak), D-arabinose, inulin, D-ribose (delayed or weak), D-glucosamine (sometimes weak), D-glucitol (sometimes weak), ethanol (sometimes weak), D-Glucono-1,5-lactone (variable), succinate (positive), DL-lactate (sometimes weak), D-gluconate, ribitol (sometimes weak), maltose, citrate (variable), soluble starch (delayed), xylitol (sometimes delayed), D-galacturonate, arbutin, DL-malic acid, L-arabinitol (weak), D-glucuronate. The following sole carbon compounds cannot be assimilated: Lactose, L-sorbose, glycerol, methanol, hexadecane, erythritol, levulinic acid, butane-2,3-diol, isopropanol, propane-1,2-diol. The following sole nitrogen compounds can be assimilated: Ammonium sulphate, L-lysine, ethylamine hydrochloride (delayed or delayed and weak), cadaverine dihydrochloride (delayed), potassium nitrate (sometimes delayed). The following sole nitrogen compound cannot be assimilated: sodium nitrite. Growth in vitamin-free medium is positive. Growth is negative or weak at 25 °C, but negative at 28 °C. Optimal growth temperature is between 4 °C and 20 °C. Growth in 0.01 % cycloheximide (w/v) is negative. Growth on 10 % NaCl + 5 % glucose medium (w/v) and 50 % glucose agar (w/w) are negative. Extracellular starch-like compounds are produced. Urease reaction is positive. Diazonium Blue B reaction is positive.

Typus: **Spitsbergen** (Svalbard archipelago), Ny-Ålesund, obtained from seawater, Jul. 2018, *T. Zhang* (**holotype**

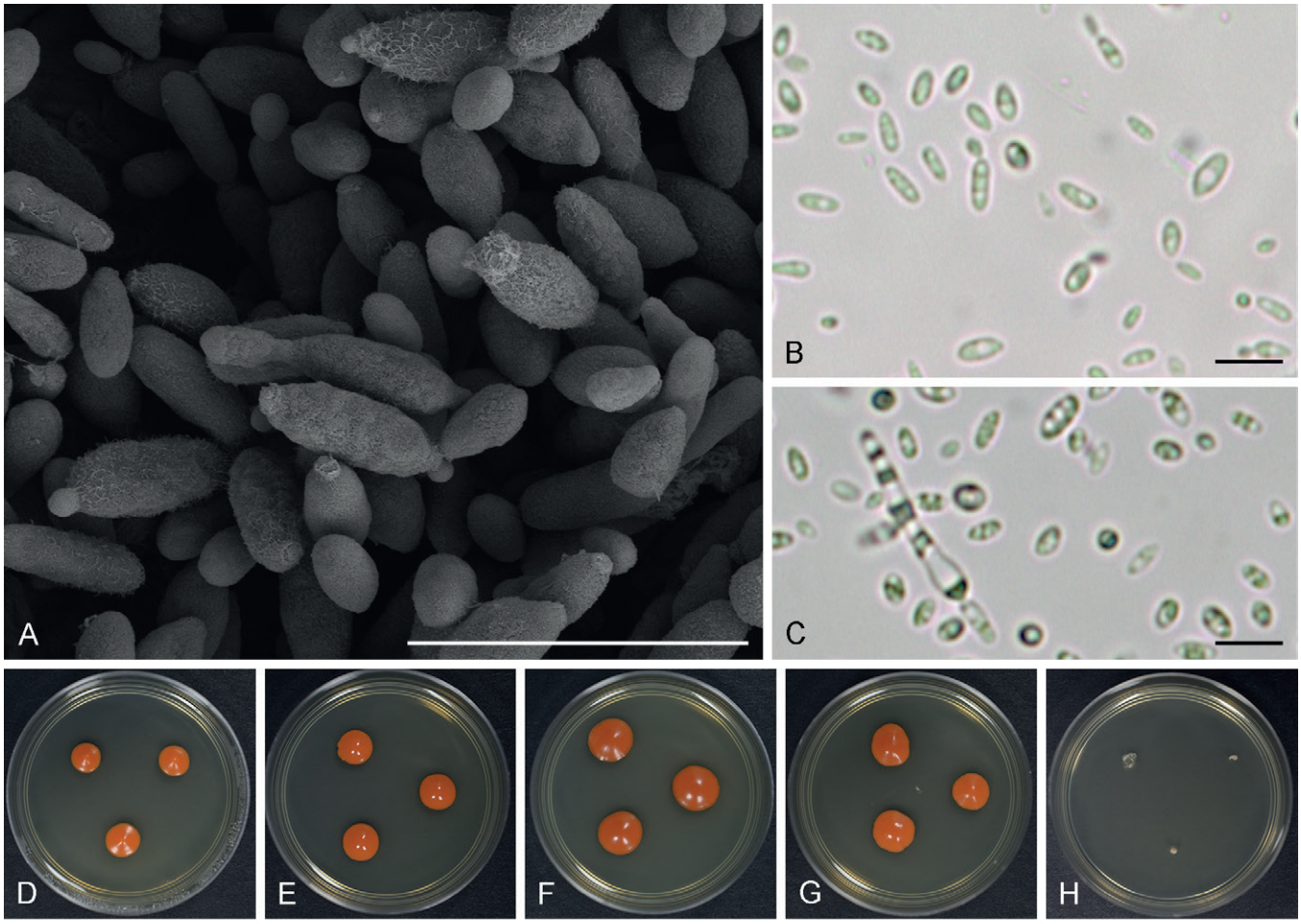

Fig. 9. *Dioszegia dongchenii* CPCC 300431^{T}. **A.** SEM image of vegetative cells grown in YM broth after 6 d at 12 °C. **B.** Light microscopy image of vegetative cells grown on YM agar after 7 d at 15 °C. **C.** Transversely septate hyphae on PDA after 2 wk at 15 °C. **D**–**H.** Views of colonies on YM agar at 4, 10, 15, 20, and 25 °C after 4 wk. Scale bars = 10 µm.

CPCC 300401^{T} preserved in a metabolically inactive state, culture ex-type CBS 18329 = ZT584).

Note: Physiologically, *Dioszegia frigidiaquatica* differs from *Dioszegia xingshanensis* in the ability to assimilate inulin, D-ribose, D-glucosamine, D-glucitol, ethanol, succinate, DL-lactate, ribitol, soluble starch, ethylamine hydrochloride, cadaverine dihydrochloride, potassium nitrate and in the inability to assimilate sodium nitrite (Wang *et al.* 2008).

Dioszegia dongchenii T. Zhang & J.J. Feng, ***sp. nov.*** MycoBank MB 843896. Fig. 9.

Etymology: The scientific epithet is in honour of Dongchen E, an expert in Chinese topography who made great contributions to China's Antarctic and Arctic exploration.

Culture characteristics: After 7 d in YM broth at 15 °C, a sediment and a ring are formed. After 28 d in YM broth at 15 °C, a sediment and a pellicle can be observed. After 7 d on YM agar at 15 °C, cells are ellipsoidal to clavate, 5.2–7.7 × 2.4–4.4 µm in size, occurring single or in pairs, budding is polar. After 28 d on YM agar at 15 °C, the colonies are orange to reddish orange, butyrous, smooth, and flat. The margin is entire. Pseudohyphae or true hyphae cannot be observed in the Dalmau plate culture on CMA at 15 °C. Sexual reproduction cannot be observed on CMA, MEA, PDA, SYA, or YM agar, but transversely septate hyphae can be occasionally observed after 2 wk on PDA at 15 °C.

Physiological characteristics: All the following assimilation and related tests were conducted at 15 °C. Fermentation is negative. The following sole carbon compounds can be assimilated: Glucose, melibiose, galactose, sucrose, melezitose, trehalose, salicin (delayed), L-arabinose, L-rhamnose, galactitol, N-acetyl-D-glucosamine, D-mannitol, cellobiose (delayed), raffinose, D-xylose, myo-inositol (weak), D-arabinose (delayed), inulin, D-ribose, D-glucosamine, D-glucitol (weak), D-Glucono-1,5-lactone, succinate, DL-lactate (delayed and weak), D-gluconate, maltose, citrate, soluble starch (weak), xylitol (delayed), D-galacturonate, arbutin, DL-malic acid, D-glucuronate. The following sole carbon compounds cannot be assimilated: Lactose, methyl-α-D-glucoside, L-sorbose, glycerol, ethanol, methanol, hexadecane, erythritol, ribitol, levulinic acid, butane-2,3-diol, isopropanol, L-arabinitol, propane-1,2-diol. The following sole nitrogen compounds can be assimilated: Ammonium sulphate, L-lysine, cadaverine dihydrochloride, potassium nitrate (delayed). The following sole nitrogen compounds cannot be assimilated: Ethylamine hydrochloride, sodium nitrite. Growth in vitamin-free medium is delayed and weak. Growth is negative or weak at 25 °C, but negative at 28 °C. Optimal growth temperature is between 10°C and 20 °C. Growth in 0.01 % cycloheximide (w/v) is negative. Growth on 10 % NaCl + 5 % glucose medium (w/v) is weak. Growth on 50 % glucose agar (w/w) is negative. Extracellular starch-like compounds are produced. Urease reaction is positive. Diazonium Blue B reaction is positive.

Typus: **Spitsbergen** (Svalbard archipelago), Ny-Ålesund, obtained from vascular plant, Jul. 2019, *T. Zhang* (**holotype** CPCC 300431^{T} preserved in a metabolically inactive state, ex-type CBS 18330 = YC1801).

Notes: Physiologically, *Dioszegia dongchenii* differs from *Dioszegia fristingensis* and *Dioszegia antarctica* in the ability to assimilate soluble starch, potassium nitrate and in the inability to assimilate methyl-α-D-glucoside and sodium nitrite. *Dioszegia dongchenii* also sustains higher temperatures because the maximal growth temperature of both *Dioszegia fristingensis* and *Dioszegia antarctica* were less than 25 °C (Inácio *et al.* 2005, Connell *et al.* 2010).

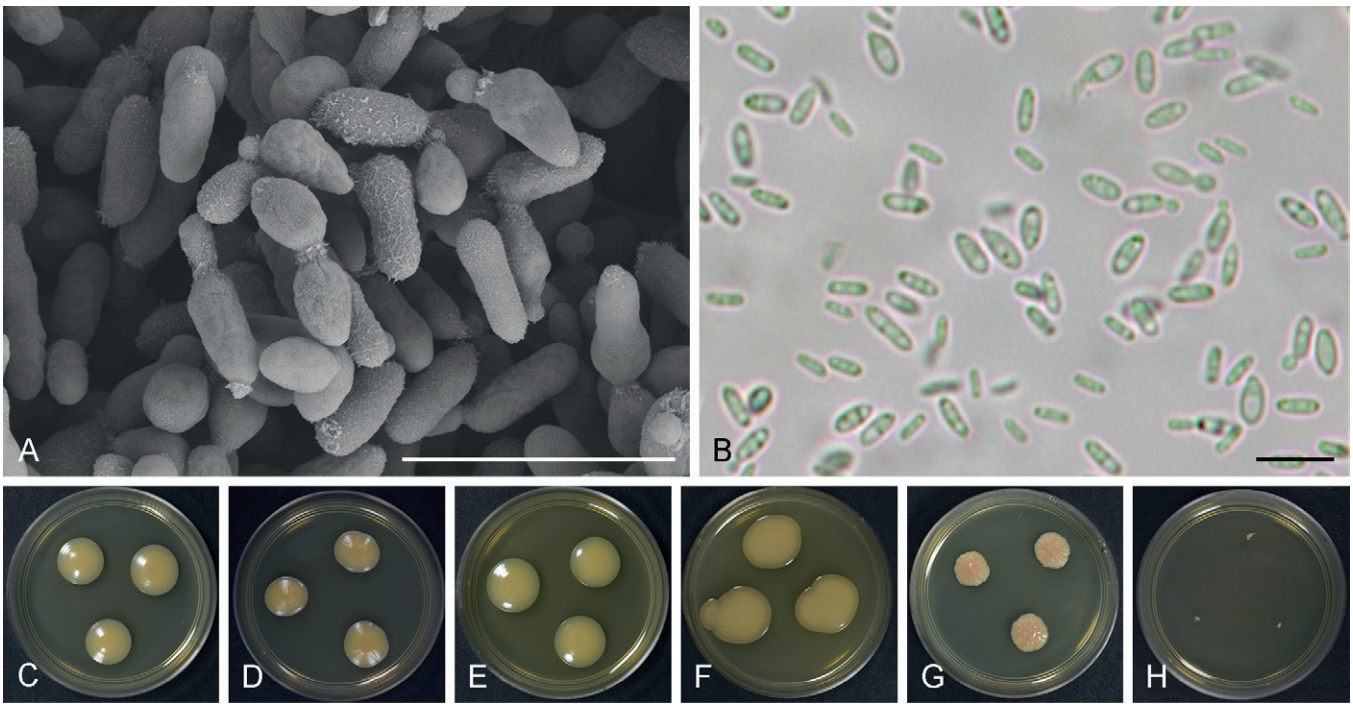

Fig. 10. *Phaeotremella polaris.* **A.** SEM image of vegetative cells grown in YM broth after 6 d at 12 °C (CPCC 300468^{T}). **B.** Light microscopy image of vegetative cells grown on YM agar after 7 d at 15 °C (CPCC 300298). **C**–**H.** Views of colonies on YM agar at 4, 10, 15, 20, 25, and 28 °C after 4 wk (CPCC 300468^{T}). Scale bars = 10 µm.

Phaeotremella polaris T. Zhang & J.J. Feng, ***sp. nov.*** MB 843891. Fig. 10.

Etymology: The scientific epithet *polaris* refers to the geographical origin from which the species was first isolated.

Culture characteristics: After 7 d in YM broth at 15 °C, a sediment is formed, a ring is formed or not. After 28 d in YM broth at 15 °C, a sediment can be observed, and a ring can be observed or not, depending on the strains. After 7 d on YM agar at 15 °C, cells are ovoid or subglobose to ellipsoidal, 4.8–7.1 × 2.7–3.6 µm in size, occurring mainly in single, occasionally in pairs, budding is mainly polar, occasionally lateral. After 28 d on YM agar at 15 °C, the colonies are yellowish white to yellow, butyrous, smooth, and flat. The margin is entire. Pseudohyphae or true hyphae cannot be observed in the Dalmau plate culture on CMA at 15 °C. Sexual reproduction cannot be observed on CMA, MEA, PDA, SYA, or YM agar.

Physiological characteristics: All the following assimilation and related tests were conducted at 15 °C. Fermentation is negative. The following sole carbon compounds can be assimilated: Glucose, melibiose, galactose (sometimes delayed), sucrose, lactose (sometimes delayed), melezitose (sometimes delayed), trehalose (sometimes delayed), salicin (sometimes delayed), L-arabinose (sometimes delayed), L-rhamnose (sometimes delayed or delayed and weak), galactitol (variable), N-acetyl-D-glucosamine, methyl-α-D-glucoside (sometimes delayed), D-mannitol (sometimes delayed and weak), cellobiose (sometimes delayed), raffinose, D-xylose, myo-inositol (delayed or delayed and weak), D-arabinose (sometimes delayed), L-sorbose (variable), inulin, D-ribose (sometimes delayed), D-glucosamine (sometimes delayed), D-glucitol (sometimes delayed or delayed and weak), glycerol (delayed or delayed and weak), ethanol (sometimes delayed or delayed and weak), D-Glucono-1,5-lactone, succinate, DL-lactate, D-gluconate (sometimes delayed), erythritol (delayed or delayed and weak), ribitol, maltose, citrate (sometimes delayed), soluble starch (variable), xylitol, D-galacturonate, arbutin, DL-malic acid, L-arabinitol, D-glucuronate. The following sole carbon compounds cannot be assimilated: Methanol, hexadecane, levulinic acid, butane-2,3-diol, isopropanol, propane-1,2-diol. The following sole nitrogen compounds can be assimilated: Ammonium sulphate, L-lysine, ethylamine hydrochloride (sometimes delayed), cadaverine dihydrochloride, potassium nitrate. The following sole nitrogen compounds cannot be assimilated: Sodium nitrite. Growth in vitamin-free medium is positive. Growth is variable at 25 °C but negative at 28 °C. Optimal growth temperature is between 4 °C and 20 °C. Growth in 0.01 % cycloheximide (w/v) is variable, while growth in 0.1 % cycloheximide (w/v) is negative. Growth on 10 % NaCl + 5 % glucose medium (w/v) and 50 % glucose agar (w/w) are negative. Extracellular starch-like compounds are not produced. Urease reaction is positive. Diazonium Blue B reaction is positive.

Typus: **Spitsbergen** (Svalbard archipelago), Ny-Ålesund, obtained from lichen, Jul. 2019, *T. Zhang* (**holotype** CPCC 300468^{T} preserved in a metabolically inactive state, culture ex-type CBS 18337 = YC85).

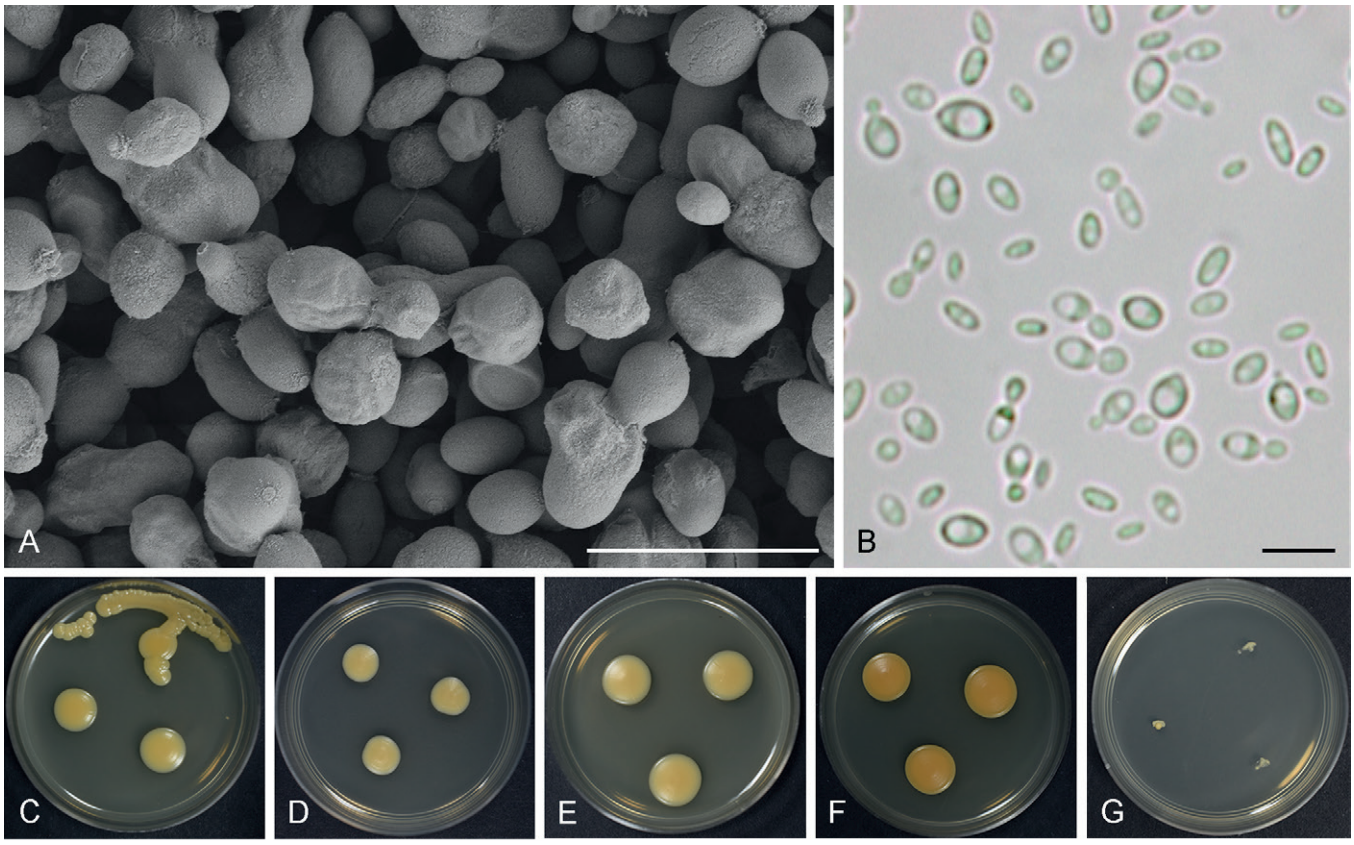

Fig. 11. *Phaeotremella nansenii* CPCC 300414^{T}. **A.** SEM image of vegetative cells grown in YM broth after 6 d at 12 °C. **B.** Light microscopy image of vegetative cells grown on YM agar after 7 d at 15 °C. **C**–**G.** Views of colonies on YM agar at 4, 10, 15, 20, and 25 °C after 4 wk. Scale bars = 10 µm.

Note: Physiologically, *Phaeotremella polaris* differs from its relative *Phaeotremella ovata* in the ability to assimilate raffinose, myo-inositol, glycerol, ethanol, succinate, DL-lactate, erythritol, and citrate (Li *et al*. 2020).

Phaeotremella nansenii T. Zhang & J.J. Feng, ***sp. nov.*** MB 843900. Fig. 11.

Etymology: The scientific epithet *nansenii* refers to Fridtjof Nansen, an explorer from Norway, who led the team to accomplish the first crossing of the Greenland interior and made great contributions towards polar research and expedition.

Culture characteristics: After 7 d in YM broth at 15 °C, a sediment is formed. After 28 d in YM broth at 15 °C, a sediment and a very weak ring can be observed. After 7 d on YM agar at 15 °C, cells are subglobose to ellipsoidal, 4.8–6.7 × 3.3–5.2 µm in size, occurring single or in pairs, budding is polar. After 28 d on YM agar at 15 °C, the colonies are yellow to yellowish orange, butyrous, smooth, and flat. The margin is entire. Pseudohyphae or true hyphae cannot be observed in the Dalmau plate culture on CMA at 15 °C. Sexual reproduction cannot be observed on CMA, MEA, PDA, SYA, or YM agar.

Physiological characteristics: All the following assimilation and related tests were conducted at 15 °C. Fermentation is negative. The following sole carbon compounds can be assimilated: Glucose, melibiose, galactose, sucrose, melezitose, trehalose, salicin, L-arabinose, L-rhamnose, galactitol, methyl-α-D-glucoside, D-mannitol, cellobiose (delayed and weak), raffinose (weak), D-xylose, D-arabinose (delayed), L-sorbose, inulin, D-ribose (delayed), D-glucitol (delayed), glycerol, ethanol, D-Glucono-1,5-lactone, succinate, DL-lactate (weak), D-gluconate, ribitol (delayed and weak), maltose, citrate, xylitol (delayed), D-galacturonate, arbutin, DL-malic acid, D-glucuronate. The following sole carbon compounds cannot be assimilated: Lactose, N-acetyl-D-glucosamine, myo-inositol, D-glucosamine, methanol, hexadecane, erythritol, soluble starch, levulinic acid, butane-2,3-diol, isopropanol, L-arabinitol, propane-1,2-diol. The following sole nitrogen compounds can be assimilated: Ammonium sulphate, L-lysine, ethylamine hydrochloride (delayed), cadaverine dihydrochloride, potassium nitrate. The following sole nitrogen compound cannot be assimilated: Sodium nitrite. Growth in vitamin-free medium is positive. Growth is negative or weak at 25 °C, but negative at 28 °C. Optimal growth temperature is between 4 °C and 20 °C. Growth in 0.01 % cycloheximide (w/v) is delayed, while growth in 0.1 % cycloheximide (w/v) is negative. Growth on 10 % NaCl + 5 % glucose medium (w/v) and 50 % glucose agar (w/w) are negative. Extracellular starch-like compounds are not produced. Urease reaction is positive. Diazonium Blue B reaction is positive.

Typus: **Spitsbergen** (Svalbard archipelago), Ny-Ålesund, obtained from lichen, Jul. 2019, *T. Zhang* (**holotype** CPCC 300414^{T} preserved in a metabolically inactive state, culture ex-type CBS 18336 = YC365).

Notes: Physiologically, *Phaeotremella nansenii* differs from its closest relative *Phaeotremella camelliae* in the ability to assimilate melezitose, salicin, D-arabinose, inulin, D-glucitol, citrate, galactitol, methyl-α-D-glucoside, L-sorbose, glycerol, ethylamine hydrochloride and in the inability to assimilate myo-inositol, D-glucosamine, soluble starch and sodium nitrite (Sun *et al*. 2020).

Xiangyanghongia T. Zhang & J.J. Feng, ***gen. nov.*** MB 843942.

Etymology: The genus name refers to the name of a class of Chinese oceanographic survey and research vessels.

The genus is proposed for the separate clade represented by CPCC 300456, CPCC 300457, CPCC 300458, and CPCC 300459. The genus is mainly circumscribed by the phylogenetic analysis of the seven-genes tree, in which it occurred as a separate branch within the *Phaeotremellaceae*, *Tremellales*.

Sexual reproduction not known. Colonies yellow to yellowish white, butyrous. Budding cells present and budding is multilateral. Fermentation is negative. Cells are subglobose to globose. Pseudohyphae and true hyphae can be observed.

Type species: *Xiangyanghongia terricola* T. Zhang & J.J. Feng

Xiangyanghongia terricola T. Zhang & J.J. Feng, ***sp. nov.*** MB 843945. Fig. 12.

Etymology: The scientific epithet *terricola* refers to soil, the substrate from which the species was first described.

Culture characteristics: After 7 d in YM broth at 15 °C, a sediment and a ring are formed. After 28 d in YM broth at 15 °C, a sediment and a ring can be observed. After 7 d on YM agar at 15 °C, cells are round or subglobose to globose, 4.2–6.4 × 3.7–5.9 µm in size, occurring in single, in pairs, in a short chain with three cells or amorphous, budding is multilateral, primitive pseudohyphae and true hyphae can be directly observed. After 28 d on YM agar at 15 °C, the colonies are yellow to yellowish cream, butyrous, smooth, raised, and occasionally dome-like. The margin is entire. Pseudohyphae and true hyphae can be observed in the Dalmau plate culture on CMA after 3 wk at 15 °C. Sexual reproduction cannot be observed on CMA, MEA, PDA, SYA, or YM agar, but transversely septate hyphae can also be observed after 3 wk on MEA at 15 °C.

Physiological characteristics: All the following assimilation and related tests were conducted at 15 °C. Fermentation is negative. The following sole carbon compounds can be assimilated: Glucose, melibiose (delayed), galactose, sucrose, lactose, melezitose, trehalose, salicin (delayed), L-arabinose, L-rhamnose (delayed), galactitol (delayed), methyl-α-D-glucoside (delayed), D-mannitol, cellobiose, raffinose, D-xylose, myo-inositol (delayed and weak), D-arabinose, inulin (delayed), D-ribose (delayed and weak), D-glucitol, glycerol (delayed and weak), D-Glucono-

1,5-lactone (delayed), succinate (delayed), D-gluconate (delayed), ribitol, maltose, citrate, xylitol (delayed), DL-malic acid (delayed), L-arabinitol (delayed), D-glucuronate. The following sole carbon compounds cannot be assimilated: N-acetyl-D-glucosamine, L-sorbose, D-glucosamine, ethanol, methanol, DL-lactate, hexadecane, erythritol, soluble starch, levulinic acid, butane-2,3-diol, D-galacturonate, isopropanol, arbutin, propane-1,2-diol. The following sole nitrogen compounds can be assimilated: Ammonium sulphate, L-lysine, ethylamine hydrochloride (delayed), cadaverine dihydrochloride (delayed), potassium nitrate (weak). The following sole nitrogen compound cannot be assimilated: Sodium nitrite. Growth in vitamin-free medium is positive. Growth is negative at 25 °C. Optimal growth temperature is between 4 °C and 15 °C. Growth in 0.01 % cycloheximide (w/v) is negative. Growth on 10 % NaCl + 5 % glucose medium (w/v) and 50 % glucose agar (w/w) are negative. Extracellular starch-like compounds are produced. Urease reaction is positive. Diazonium Blue B reaction is positive.

Typus: **Antarctica**, King George Island, Fildes Region, obtained from soil, Jan. 2017, *T. Zhang* (**holotype** CPCC 300458^{T} preserved in a metabolically inactive state, culture ex-type CBS 18347 = YC799).

Piskurozyma viscida T. Zhang & J.J. Feng, ***sp. nov.*** MB 843903. Fig. 13.

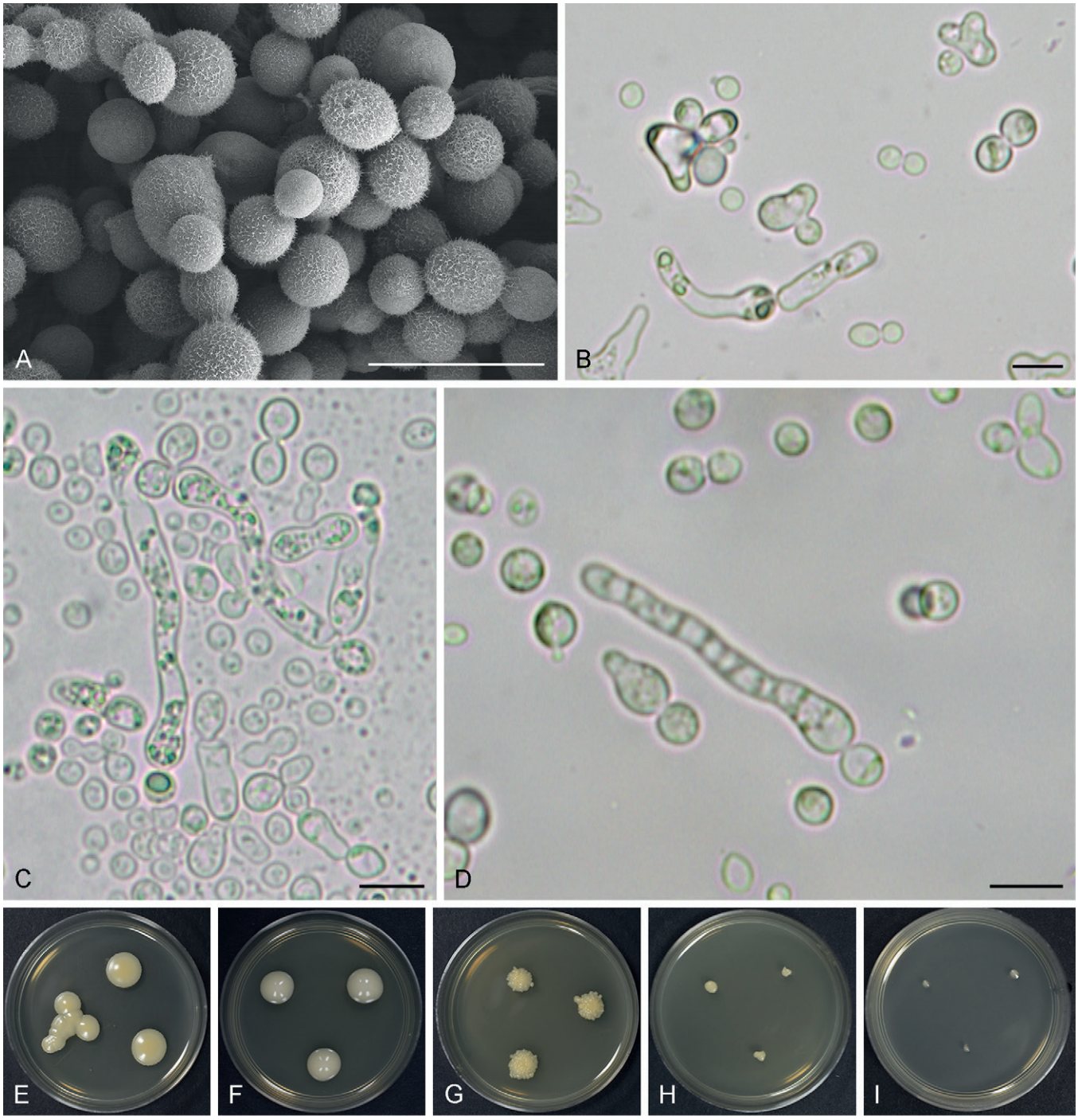

Fig. 12. *Xiangyanghongia terricola* CPCC 300458^{T}. **A.** SEM image of vegetative cells grown in YM broth after 6 d at 12 °C. **B.** Light microscopy image of vegetative cells grown on YM agar after 7 d at 15 °C. **C.** Pseudohyphae in the Dalmau plate culture in CMA after 3 wk at 15 °C. **D.** Transversely septate hyphae after 3 wk on MEA at 15 °C. **E–I**. Views of colonies on YM agar at 4, 10, 15, 20, and 25 °C after 4 wk. Scale bars = 10 µm.

Etymology: The scientific epithet *viscida* refers to the viscidity of the species on agar medium.

Culture characteristics: After 7 d in YM broth at 15 °C, a sediment is formed. After 28 d in YM broth at 15 °C, a sediment and occasionally partial pellicle can be observed. After 7 d on YM agar at 15 °C, cells are subglobose to ellipsoidal, 7.0–9.3 × 3.6–8.0 µm in size, occurring mainly in single, occasionally in pairs, budding is polar. After 28 d on YM agar at 15 °C, the colonies are cream to white, butyrous, smooth, flat, and somewhat dull. The margin is entire. Pseudohyphae or true hyphae cannot be observed in the

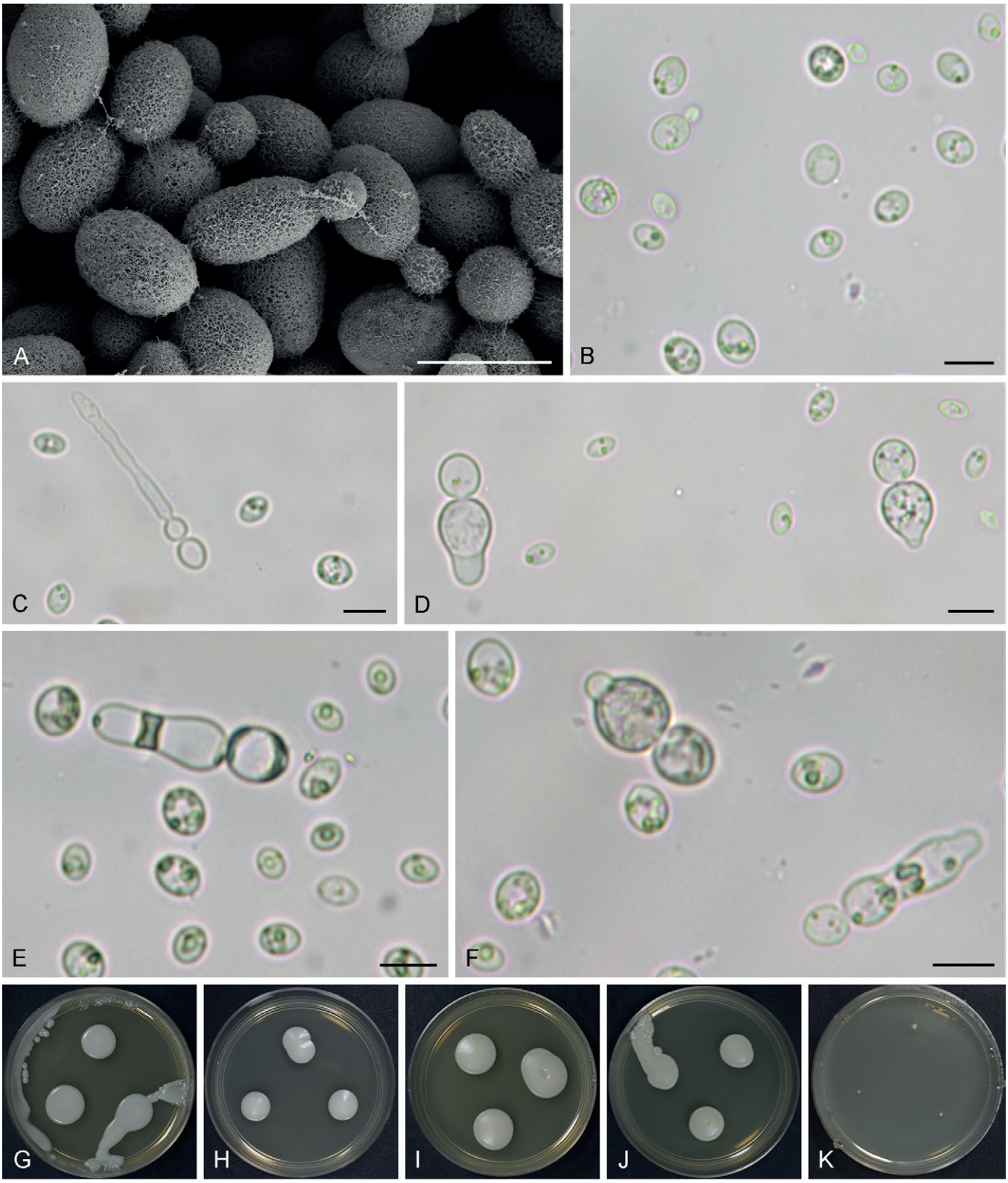

Fig. 13. *Piskurozyma viscida*. **A.** SEM image of vegetative cells grown in YM broth for 6 d at 12 °C (CPCC 300400^T). **B.** Light microscopy image of vegetative cells grown on YM agar after 7 d at 15 °C (CPCC 300296). **C.** Hyphae from two conjugated vegetative yeast cells on SYA after 3 wk at 15 °C (CPCC 300296). **D**. Calabash-like budding vegetative cells on SYA after 2 wk at 15 °C (CPCC 300296). **E**. Transversely septate hyphae on CMA after 3 wk at 15 °C (CPCC 300296). **F.** Chlamydospore-like cells on CMA after 3 wk at 15 °C (CPCC 300296). **G–K.** Views of cultures on YM agar at 4, 10, 15, 20, and 25 °C after 4 wk (CPCC 300400^T). Scale bars: A = 5 µm; B–F = 10 µm.

Dalmau plate culture on CMA at 15 °C. Chlamydospore-like cells are observed on CMA after 3 wk at 15 °C and calabash-like budding vegetative cells are observed on SYA after 2 wk at 15 °C. Sexual reproduction cannot be observed on CMA, MEA, PDA, SYA, or YM agar, but aseptate hyphae derived from two conjugated vegetative yeast cells can be observed on SYA after 3 wk at 15 °C. Additionally, transversely septate hyphae derived from teliospore-like vegetative yeast cells can also be observed on CMA after 3 wk at 15 °C.

Physiological characteristics: All the following assimilation and related tests were conducted at 15 °C. Fermentation is negative. The following sole carbon compounds can be assimilated: Glucose, melibiose (variable), galactose (delayed), sucrose (variable), lactose (variable), melezitose (variable), trehalose (sometimes delayed), salicin, L-arabinose, L-rhamnose (sometimes delayed and weak), N-acetyl-D-glucosamine (sometimes delayed and weak), cellobiose (delayed), raffinose (delayed or weak), D-xylose, myo-inositol (sometimes delayed), D-arabinose (delayed), inulin (delayed and weak), D-ribose (delayed or weak), D-glucosamine (delayed or weak), D-glucitol (sometimes delayed), ethanol (sometimes delayed and weak), D-Glucono-1,5-lactone, succinate (delayed or weak), DL-lactate (weak), D-gluconate (variable), maltose (variable), citrate (delayed), xylitol (variable), D-galacturonate, arbutin (delayed or delayed and weak), DL-malic acid, D-glucuronate. The following sole carbon compounds cannot be assimilated: Galactitol, methyl-α-D-glucoside, D-mannitol, L-sorbose, glycerol, methanol, hexadecane, erythritol, ribitol, soluble starch, levulinic acid, butane-2,3-diol, isopropanol, L-arabinitol, propane-1,2-diol. The following sole nitrogen compounds can be assimilated: Ammonium sulphate, L-lysine, ethylamine hydrochloride (sometimes delayed and weak), cadaverine dihydrochloride, potassium nitrate. The following sole nitrogen compound cannot be assimilated: Sodium nitrite. Growth in vitamin-free medium is positive or delayed. Growth is negative at 25 °C. Optimal growth temperature is between 4 °C and 15 °C. Growth in 0.01 % cycloheximide (w/v) is either delayed or delayed and weak, while growth in 0.1 % cycloheximide (w/v) is negative. Growth on 10 % NaCl + 5 % glucose medium (w/v) and 50 % glucose agar (w/w) are negative. Extracellular starch-like compounds are not produced. Urease reaction is positive. Diazonium Blue B reaction is positive.

Typus: **Antarctica**, King George Island, Fildes Region, obtained from soil, Jan. 2017, *T. Zhang* (**holotype** CPCC 300400^{T} preserved in a metabolically inactive state, culture ex-type CBS 18362 = ZT582).

Note: Physiologically, *Piskurozyma viscida* differs from its closest relative *Piskurozyma linzhiensis* in the ability to assimilate salicin, N-acetyl-D-glucosamine, D-glucosamine, citrate and in the inability to assimilate methylα-D-glucoside, D-mannitol, L-sorbose, glycerol, ribitol, soluble starch and sodium nitrite. Additionally, *Piskurozyma viscida* can grow on vitamin-free medium (Jiang *et al*. 2024)

New taxa in *Microbotryomycetes* (*Pucciniomycotina*)

Skadia T. Zhang & J.J. Feng, ***gen. nov.*** MB 843923.

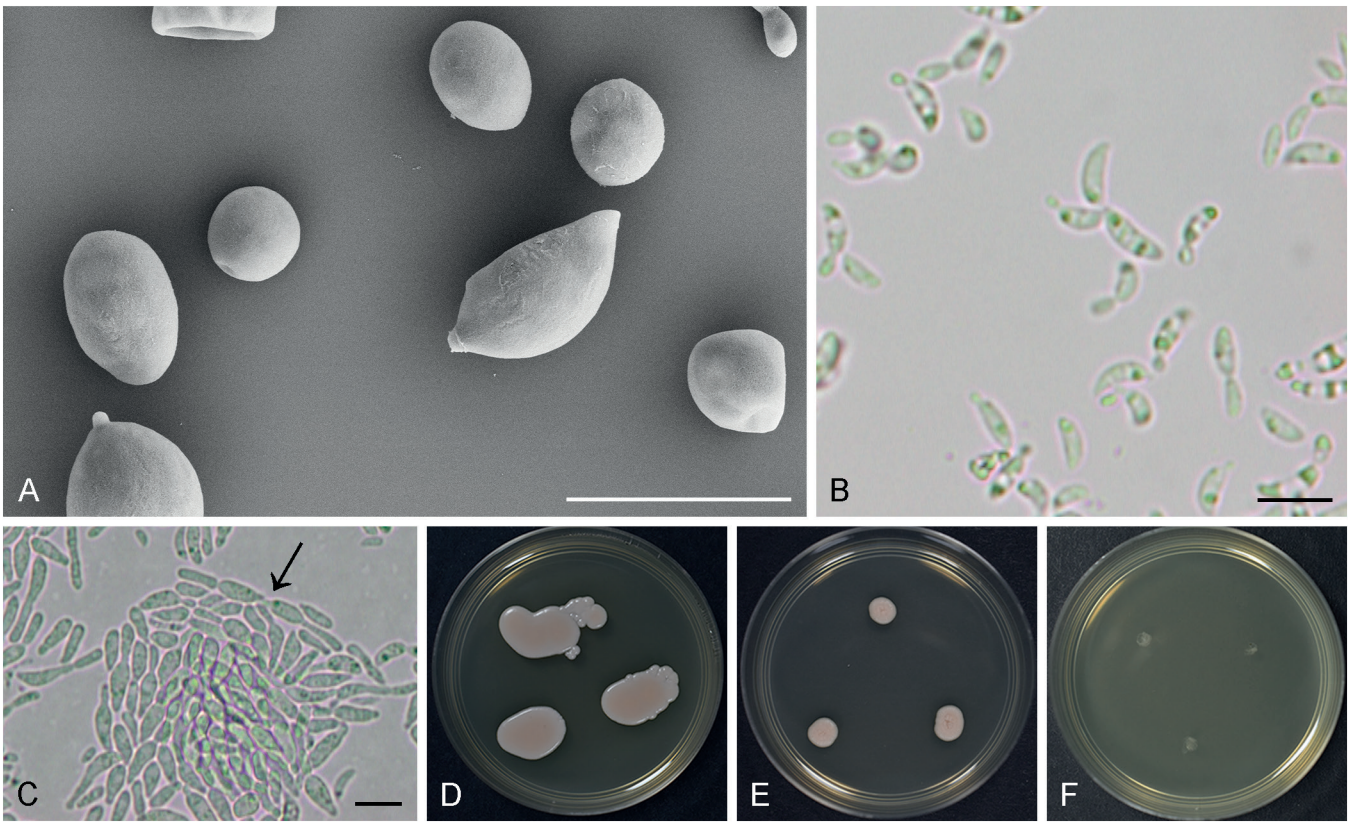

Fig. 14. *Skadia corniformis* CPCC 300470^{T}. **A.** SEM image of vegetative cells grown in YM broth after 6 d at 4 °C. **B.** Light microscopy image of vegetative cells grown on YM agar after 7 d at 8 °C. **C.** Primitive pseudohyphae in the Dalmau plate culture on CMA at 8 °C after 3 wk (see arrow). **D**–**F.** Views of cultures on YM agar at 4, 10, and 15 °C after 4 wk. Scale bars = 10 µm.

Etymology: The genus name refers to Skaði, a goddess associated with winter in ancient Norse mythology.

The genus is proposed according to the circumscription of strain CPCC 300470 in the seven-gene phylogeny with additional strains CPCC 300506, CPCC 300509, and CPCC 300515 in the concatenated ITS-D1/D2 tree. This genus is a new member of the family *Camptobaisiaceae*.

The colonies are mainly white to pinkish white, butyrous. Budding cells present and budding is polar. Fermentation is negative. A single cell is mainly cornute. Pseudohyphae may be observed in the Dalmau plate. Strictly psychrophilic. Sexual reproduction not known.

Type species: *Skadia corniformis* T. Zhang & J.J. Feng

Skadia corniformis T. Zhang & J.J. Feng, ***sp. nov.*** MB 843924. Fig. 14.

Etymology: The scientific epithet *corniformis* refers to the corniform morphology of the cells of type strain by microscopic observation.

Culture characteristics: After 7 d in YM broth at 8 °C, a sediment is formed. After 28 d in YM broth at 8 °C, a sediment can be observed. After 7 d on YM agar at 8 °C, cells are mainly cornute, occasionally globose to subglobose or ellipsoidal, 5.5–9.1 × 2.0–3.1 µm in size, occurring mainly in pairs, occasionally single or in triple, budding is polar. After 28 d on YM agar at 8 °C, the colonies are white to pinkish white, butyrous, smooth, and flat. The margin is entire. Primitive pseudohyphae can be occasionally observed in the Dalmau plate culture on CMA at 8 °C after 3 wk, true hyphae cannot be observed. Sexual reproduction cannot be observed on CMA, MEA, PDA, SYA, or YM agar.

Physiological characteristics: All the following assimilation and related tests were conducted at 8 °C. Fermentation is negative. The following sole carbon compounds can be assimilated: Glucose, melibiose (delayed and weak), galactose, sucrose (delayed), lactose (delayed and weak), melezitose, trehalose, salicin (delayed), L-arabinose (delayed), galactitol (delayed and weak), D-mannitol (delayed), cellobiose (delayed), D-xylose (delayed), L-sorbose (delayed and weak), inulin (delayed), D-glucitol (delayed and weak), succinate (delayed and weak), D-gluconate (delayed and weak), ribitol (delayed and weak), maltose (delayed), soluble starch (delayed), arbutin (delayed and weak), L-arabinitol (delayed and weak). The following sole carbon compounds cannot be assimilated: L-rhamnose, N-acetyl-D-glucosamine, methyl-α-D-glucoside, raffinose, myo-inositol, D-arabinose, D-ribose, D-glucosamine, glycerol, ethanol, methanol, D-Glucono-1,5-lactone, DL-lactate, hexadecane, erythritol, citrate, xylitol, levulinic acid, butane-2,3-diol, D-galacturonate, isopropanol, DL-malic acid, D-glucuronate, propane-1,2-diol. The following sole nitrogen compounds can be assimilated: Ammonium sulphate (delayed), L-lysine (delayed), ethylamine hydrochloride (delayed), cadaverine dihydrochloride (delayed and weak), potassium nitrate (delayed). The following sole nitrogen compound cannot be assimilated: Sodium nitrite. Growth in vitamin-free medium is negative. Growth is negative at 15 °C. Optimal growth temperature is between 4 °C and 10 °C. Growth in 0.01 % cycloheximide (w/v) is negative. Growth on 10 % NaCl + 5 % glucose medium (w/v) is positive and growth on 50 % glucose agar (w/w) is negative. Extracellular starch-like compounds are not produced. Urease reaction is positive. Diazonium Blue B reaction is positive.

Typus: **Spitsbergen** (Svalbard archipelago), Ny-Ålesund, obtained from freshwater, Jul. 2018, *T. Zhang* (**holotype** CPCC 300470^{T} preserved in a metabolically inactive state, culture ex-type CBS 18348 = ZT871).

Skadia rubropurpurea T. Zhang & J.J. Feng, ***sp. nov.*** MB 858795. Fig. 15.

Etymology: The scientific epithet *rubropurpurea* refers to the purplish pink colour of the colony of the type strain on agar medium.

Culture characteristics: After 7 d in YM broth at 8 °C, a sediment is formed. After 28 d in YM broth at 8 °C, a sediment can be observed. After 7 d on YM agar at 8 °C, cells are ovoid to ellipsoidal, 4.7–6.9 × 2.8–4.7 µm in size, occurring mainly single or in pairs, occasionally in triple or in a short chain with three to four vegetative yeast cells, budding is polar. After 28 d on YM agar at 8 °C, the colonies are pinkish white to pink or purplish pink, butyrous, surface rough with round spike-like bulge, usually raised and occasionally dome-like. The margin is entire. True hyphae can be observed in the Dalmau plate culture on CMA at 8 °C after 3 wk, pseudohyphae cannot be observed. Teliospores and hyphae can be observed on CMA, SYA, PDA, and YM agar after 3 wk at 8 °C. Teliospores terminal, globose to subglobose, 9.6–10.3 × 7.9–9.3 µm in size, occasionally with one to three or four vegetative yeast cells budding around. Multiple septate hyphae or yeast cells may germinate from the same position in teliospores, with or without clamp collection, clavate, usually with slightly curved, apex relatively narrow compared with the basal, 16–31 µm in length and 3–5 µm in width.

Physiological characteristics: All the following assimilation and related tests were conducted at 8 °C. Fermentation is negative. The following sole carbon compounds can be assimilated: Glucose (delayed), melibiose (delayed and weak), galactose (delayed), melezitose (delayed and weak), trehalose (delayed), salicin (delayed), L-arabinose (delayed and weak), galactitol (delayed and weak), D-mannitol (weak), cellobiose (delayed), D-arabinose (delayed), D-ribose (delayed and weak), glycerol (delayed and weak), ribitol (delayed and weak), L-arabinitol (delayed and weak). The following sole carbon compounds cannot be assimilated: Sucrose, lactose, L-rhamnose, N-acetyl-D-glucosamine, methyl-α-D-glucoside, raffinose, D-xylose, myo-inositol, L-sorbose, inulin, D-glucosamine, D-glucitol, ethanol, methanol, D-Glucono-1,5-lactone, succinate, DL-lactate, D-gluconate, hexadecane, erythritol, maltose, citrate, soluble starch, xylitol, levulinic acid, butane-2,3-diol, D-galacturonate, isopropanol, arbutin, DL-malic acid, D-glucuronate, propane-1,2-diol. The following sole nitrogen compounds can be assimilated: Ammonium sulphate (delayed), L-lysine (delayed), ethylamine hydrochloride (delayed), cadaverine dihydrochloride (delayed), potassium

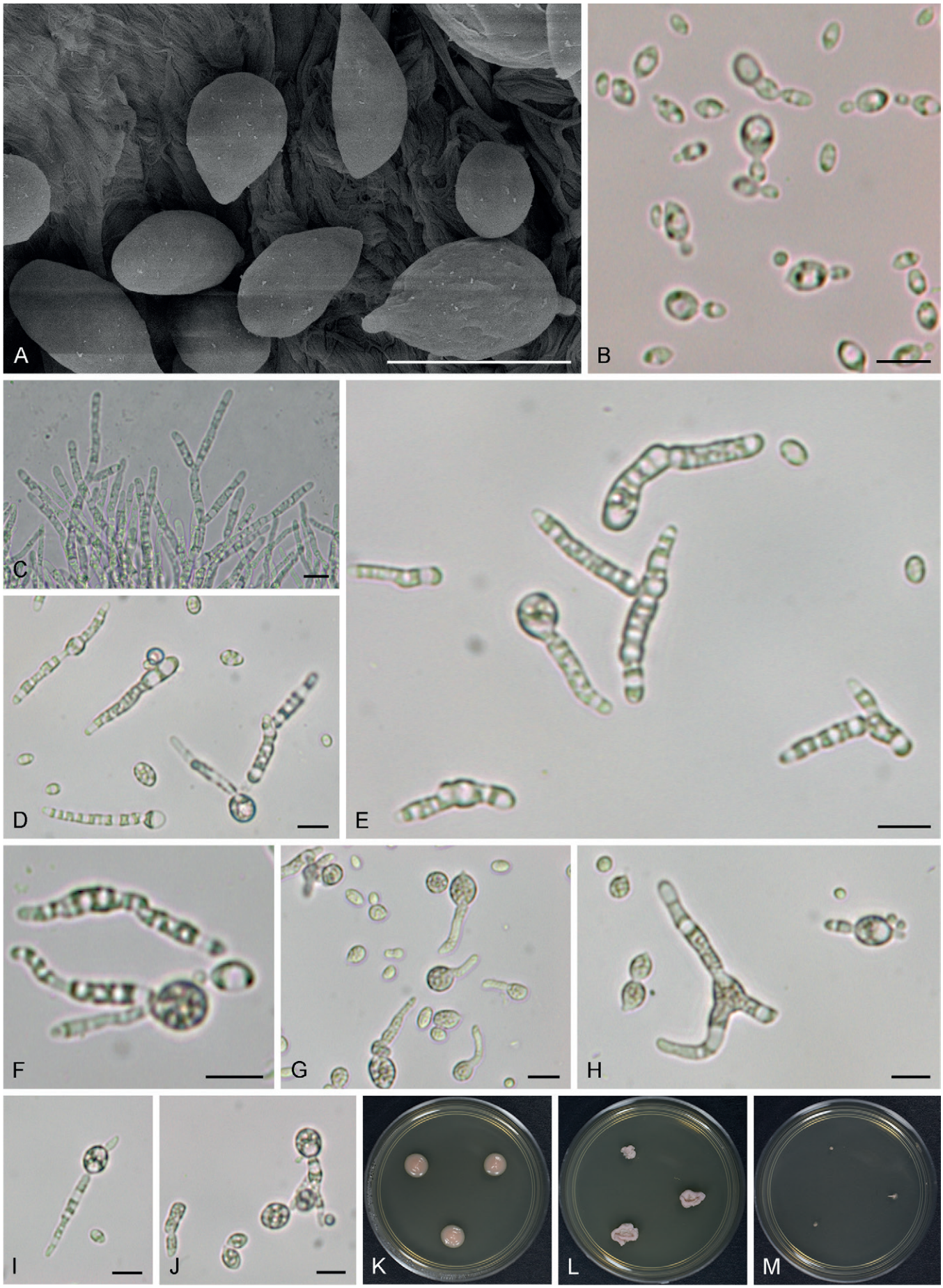

Fig. 15. *Skadia rubropurpurea* CPCC 300396[T]. **A.** SEM image of vegetative cells grown in YM broth after 6 d at 10 °C. **B.** Light microscopy image of vegetative cells grown on YM agar after 7 d at 8 °C. **C.** True hyphae in the Dalmau plate culture on CMA at 8 °C after 3 wk. **D, E.** Teliospores with hyphae on CMA after 3 wk at 8 °C. **F.** Teliospores with hyphae on YM agar after 3 wk at 8 °C. **G**, **H.** Teliospores with hyphae and three budding yeast cells on SYA after 3 wk at 8 °C. **I, J.** Teliospores with hyphae and one budding yeast cell on PDA after 3 wk at 8 °C. **K–M.** Views of cultures on YM agar at 4, 10, and 15 °C after 4 wk. Scale bars: A = 5 µm; B–J = 10 µm.

nitrate (delayed). The following sole nitrogen compound cannot be assimilated: Sodium nitrite. Growth in vitamin-free medium is delayed and weak. Growth is negative at 15 °C. Optimal growth temperature is between 4 °C and 10 °C. Growth in 0.01 % cycloheximide (w/v) is weak, while growth in 0.1 % cycloheximide (w/v) is negative. Growth on 10 % NaCl + 5 % glucose medium (w/v) and 50 % glucose agar (w/w) are negative. Extracellular starch-like compounds are not produced. Urease reaction is positive. Diazonium Blue B reaction is positive.

Typus: **Spitsbergen** (Svalbard archipelago), Ny-Ålesund, obtained from soil, Jul. 2019, *T. Zhang* (**holotype** CPCC 300396^{T} preserved in a metabolically inactive state, culture ex-type CBS 18373 = ZT508).

Xuelongia T. Zhang & J.J. Feng, ***gen. nov.*** MB 843914.

Etymology: The genus name refers to MV Xuelong, the icebreaking and re-supply vessel in the Arctic and Antarctic scientific research of China.

The genus is proposed according to the circumscription of strain CPCC 300512 in the seven-gene phylogeny with additional strains CPCC 300450, CPCC 300510, and CPCC 300521 in the concatenated ITS-D1/D2 tree. This genus is a new member of the family *Camptobaisiaceae*. *Xuelongia* shares similar morphological characteristics with *Cryolevonia*, but differs from *Cryolevonia schafbergenis* with smaller size cells and the inability to produce pseudohyphae and it differs from *Cryolevonia giraudoae* in the mode of budding. Physiologically, *Xuelongia* differs from *Cryolevonia* in the ability to assimilate melibiose, trehalose and in the inability to assimilate sodium nitrite, some strains in *Xuelongia* can sustain over 18 °C, higher than the maximum temperature for growth in *Cryolevonia*.

The colonies are mainly cream to yellowish or pinkish white, rough. Budding cells present and budding is polar. Fermentation is negative. A single cell is mainly ovoid or ellipsoidal to short clavate. Pseudohyphae cannot be observed in the Dalmau plate. Sexual reproduction cannot be observed, but teliospores or teliospore-like structures can be observed in some strains.

Type species: *Xuelongia filamentosa* T. Zhang & J.J. Feng

Xuelongia filamentosa T. Zhang & J.J. Feng, ***sp. nov.*** MB 858796. Fig. 16.

Etymology: The scientific epithet *filamentosa* refers to the appearance of small filament-like granules constituted by yeast cells on agar medium.

Culture characteristics: After 7 d in YM broth at 8 °C, a sediment is formed. After 28 d in YM broth at 8 °C, a sediment and occasionally a partial ring or a very weak pellicle can be observed, depending on the strains. After 7 d on YM agar at 8 °C, cells are ovoid or ellipsoidal to short clavate, 4.5–7.1 × 2.8–4.8 µm in size, occurring mainly single or in pairs, occasionally in a short chain with several vegetative yeast cells, budding is polar. After 28 d on YM agar at 8 °C, the colonies are pale cream to slightly yellowish white to slightly pinkish white, butyrous, rough and ridged, usually raised and dome-like. The margin is entire, occasionally wrinkled or tassel-like. Pseudohyphae cannot be observed in the Dalmau plate culture on CMA at 8 °C, but elongated hyphae can be observed after 2 wk. Sexual reproduction cannot be observed on CMA, MEA, PDA, SYA, or YM agar. Long multinucleate septate hyphae can be observed on SYA and YM agar after 3 wk. Inflated conjugated cells and septate hyphae germinated from an individual vegetative yeast cell can be observed on SYA after 2 wk at 8 °C. Teliospores can be observed after 2–3 wk at 12 °C on PDA, SYA and YM agar without the isolation of mating, terminal, globose to subglobose, 12–13 µm diam., usually with long or short hyphae germinated.

Physiological characteristics: All the following assimilation and related tests were conducted at 8 °C. Fermentation is negative. The following sole carbon compounds can be assimilated: Glucose (delayed), melibiose (delayed and weak), galactose (variable), sucrose (delayed), melezitose (delayed), trehalose (delayed), salicin (delayed), galactitol (variable), D-mannitol (variable), cellobiose (variable), raffinose (delayed or weak), L-sorbose (variable), inulin (delayed or delayed and weak), glycerol (variable), ribitol (variable), maltose (variable), soluble starch (variable), D-galacturonate (variable), DL-malic acid (variable), L-arabinitol (variable), propane-1,2-diol (variable). The following sole carbon compounds cannot be assimilated: Lactose, L-arabinose, L-rhamnose, N-acetyl-D-glucosamine, methyl-α-D-glucoside, D-xylose, myo-inositol, D-arabinose, D-ribose, D-glucosamine, D-glucitol, ethanol, methanol, D-Glucono-1,5-lactone, succinate, DL-lactate, D-gluconate, hexadecane, erythritol, citrate, xylitol, levulinic acid, butane-2,3-diol, isopropanol, arbutin, D-glucuronate. The following sole nitrogen compounds can be assimilated: Ammonium sulphate (delayed), L-lysine (delayed), ethylamine hydrochloride (delayed or delayed and weak), cadaverine dihydrochloride (delayed), potassium nitrate (delayed). The following sole nitrogen compound cannot be assimilated: Sodium nitrite. Growth in vitamin-free medium is delayed. Growth is very weak or negative at 20 °C, but negative at 25 °C. Optimal growth temperature is between 4 °C and 10 °C. Growth in 0.01 % cycloheximide (w/v) is negative. Growth in 10 % NaCl + 5 % glucose medium (w/v) is weak or negative. Growth on 50 % glucose agar (w/w) is negative. Extracellular starch-like compounds are not produced. Urease reaction is variable. Diazonium Blue B reaction is positive.

Typus: **Spitsbergen** (Svalbard archipelago), Ny-Ålesund, obtained from freshwater, Jul. 2018, *T. Zhang* (**holotype** CPCC 300512^{T} preserved in a metabolically inactive state, culture ex-type CBS 18326 = YC1057).

Glaciozyma elongata J.J. Feng & T. Zhang, ***sp. nov.*** MB 858798. Fig. 17.

Etymology: The scientific epithet *elongata* refers to the elongated shape of vegetative cells by microscopic observation.

Culture characteristics: After 7 d in YM broth at 15 °C, a sediment and occasionally a weak ring are formed. After 28 d in YM broth at 15 °C, a sediment and a ring with occasionally

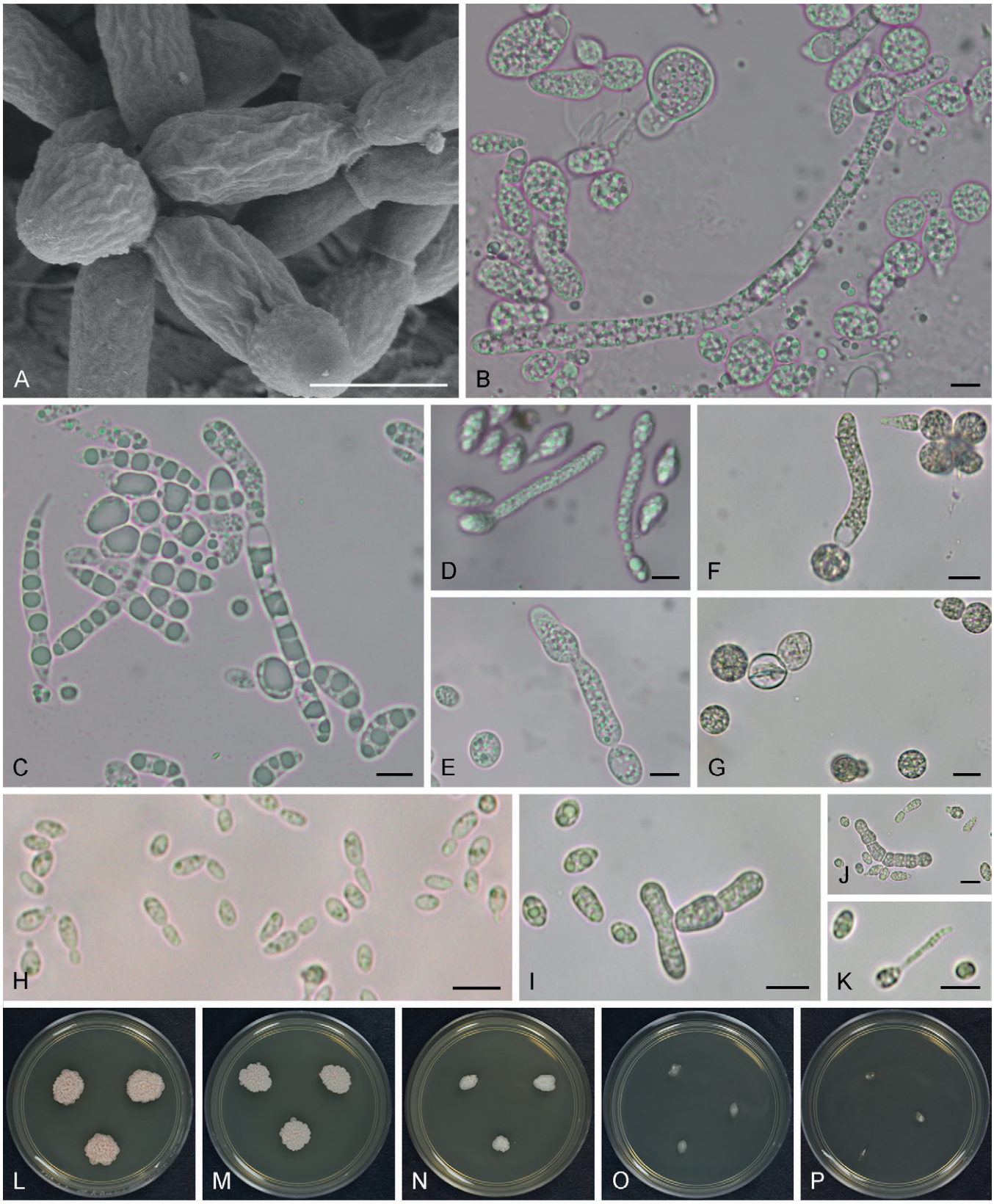

Fig. 16. *Xuelongia filamentosa*. **A.** SEM image of vegetative cells grown in YM broth after 6 d at 12 °C (CPCC 300512^{T}). **B.** Elongated hyphae in the Dalmau plate culture on CMA at 8 °C after 3 wk (CPCC 300512^{T}). **C–E.** Long multinucleate septate hyphae and pseudohyphae on PDA, SYA, and YM agar at 8 °C after 3 wk (CPCC 300512^{T}). **F**, **G.** Teliospores with or without hyphae and basidia on PDA after 3 wk at 12 °C (CPCC 300512^{T}). **H.** Light microscopy image of vegetative cells grown on YM agar after 7 d at 8 °C (CPCC 300450). **I**, **J.** Inflated conjugated cells on SYA after 2 wk at 8 °C (CPCC 300450). **K.** Hyphae germinated from a vegetative yeast cell on SYA after 2 wk at 8 °C (CPCC 300450). **L**–**P.** Views of colonies on YM agar at 4, 10, 15, 20, and 25 °C after 4 wk (CPCC 300512^{T}). Scale bars: A = 5 µm; B–K = 10 µm.

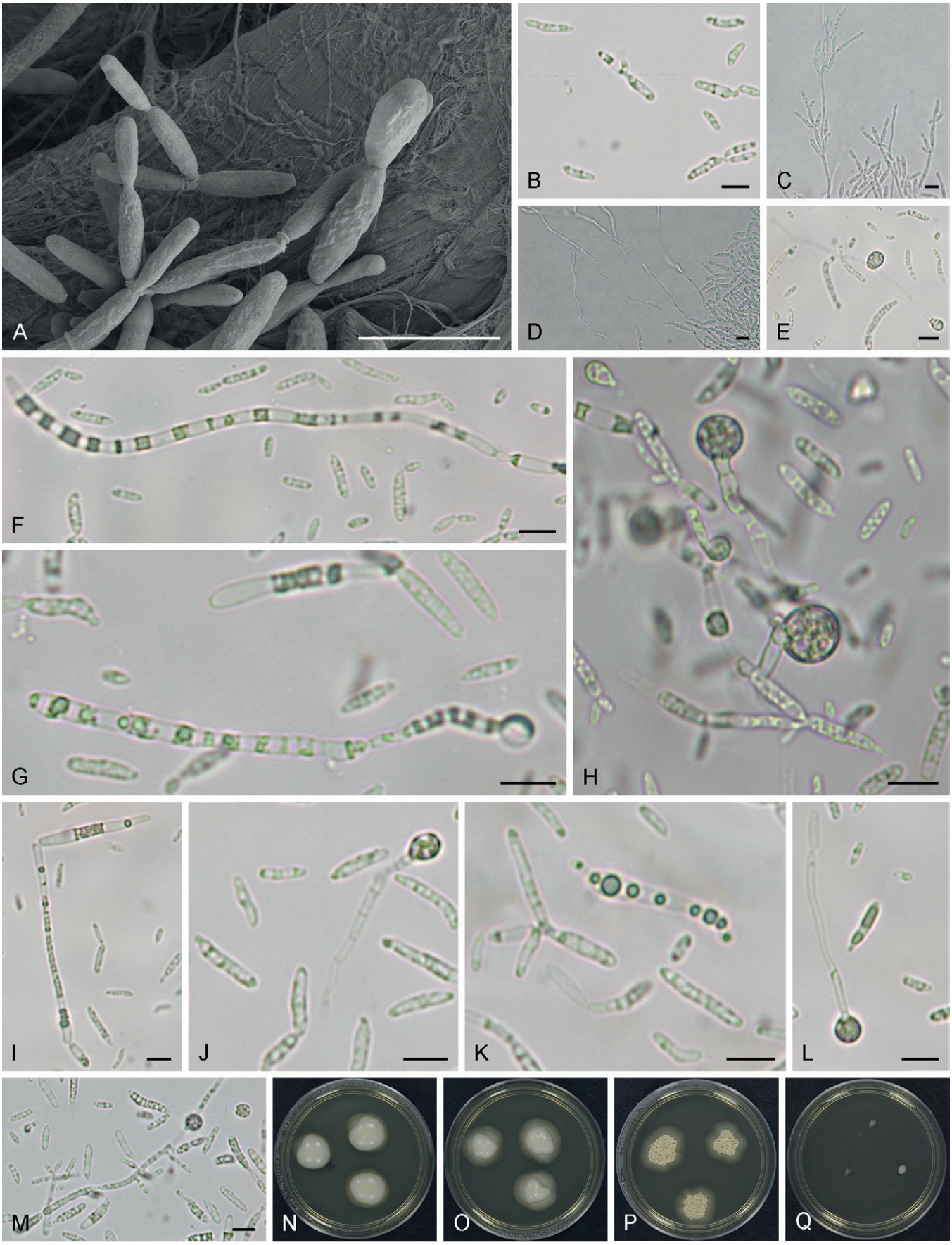

Fig. 17. *Glaciozyma elongata* CPCC 300077^{T}. **A.** SEM image of vegetative cells grown in YM broth after 7 d at 15 °C. **B.** Light microscopy image of vegetative cells grown on YM agar after 7 d at 15 °C. **C.** Pseudohyphae in the Dalmau plate culture on CMA at 15 °C after 2 wk. **D.** True hyphae in the Dalmau plate culture on CMA at 15 °C after 2 wk. **E.** Teliospore with hyphae on CMA after 3 wk at 15 °C. **F.** Transversely septate hyphae on CMA after 3 wk at 15 °C. **G.** Teliospore with transversely septate multinucleate hyphae on SYA after 3 wk at 15 °C. **H.** Terminal teliospore and lateral teliospore on SYA after 3 wk at 15 °C. **I.** Hyphae on SYA after 3 wk at 15 °C. **J.** Teliospore with hyphae on YM agar after 3 wk at 15 °C. **K.** Multinucleate hyphae on YM agar after 3 wk at 15 °C. **L.** Teliospore with hyphae on MEA after 3 wk at 15 °C. **M.** Teliospores with transversely septate hyphae on PDA after 5 wk at 15 °C. **N**–**Q.** Views of colonies on YM agar at 4, 10, 15, and 20 °C after 4 wk. Scale bars = 10 µm.

a pellicle can be observed, depending on the strains. After 7 d on YM agar at 15 °C, cells are long ellipsoidal to long clavate or elongate, 9.0–14.6 × 3.0–3.9 µm in size, occurring in single, in pairs or in multiple, occasionally in a chain with several cells, budding is polar. After 28 d on YM agar at 15 °C, the colonies are cream or white to yellowish white, dry butyrous, dull, raised, rough, and ridged. The margin is entire and usually fringed with pseudohyphae or true hyphae. Pseudohyphae and true hyphae can be observed in the Dalmau plate culture on CMA at 15 °C after 2 wk. Teliospores and hyphae can be observed on CMA, MEA, PDA, SYA, and YM agar after 2–4 wk at 15 °C. Teliospores terminal or lateral, globose, or subglobose, diameter varies from about 6 µm to over 12 µm. Hyphae germinated from an individual vegetative yeast cell or teliospores, usually transversely septate, without obvious clamp connection, slender with slightly curved, multinucleated, 2–4 µm in width and 30–140 µm in length.

Physiological characteristics: All the following assimilation and related tests were conducted at 15 °C. Fermentation is negative. The following sole carbon compounds can be assimilated: Glucose, melibiose (variable), L-rhamnose (delayed), N-acetyl-D-glucosamine (sometimes delayed), raffinose (delayed and weak), D-xylose (variable), D-arabinose (variable), inulin (weak or delayed and weak), D-ribose (variable), D-glucosamine (delayed), glycerol (variable), ethanol (delayed), D-Glucono-1,5-lactone (variable), succinate, DL-lactate (variable), D-gluconate (variable), erythritol (variable), ribitol (variable), soluble starch (variable), D-galacturonate (variable), DL-malic acid (sometimes delayed), D-glucuronate (delayed). The following sole carbon compounds cannot be assimilated: Galactose, sucrose, lactose, melezitose, trehalose, salicin, L-arabinose, galactitol, methyl-α-D-glucoside, D-mannitol, cellobiose, myo-inositol, L-sorbose, D-glucitol, methanol, hexadecane, maltose, citrate, xylitol, levulinic acid, butane-2,3-diol, isopropanol, arbutin, L-arabinitol, propane-1,2-diol. The following sole nitrogen compounds can be assimilated: Ammonium sulphate, L-lysine, ethylamine hydrochloride, cadaverine dihydrochloride, sodium nitrite, potassium nitrate. Growth in vitamin-free medium is positive. Growth is negative or weak at 20 °C, no growth observed at 25 °C. Optimal growth temperature is between 4 °C and 15 °C. Growth in 0.01 % cycloheximide (w/v) is negative. Growth on 10 % NaCl + 5 % glucose medium (w/v) and 50 % glucose agar (w/w) are negative. Extracellular starch-like compounds are not produced. Urease reaction is variable. Diazonium Blue B reaction is positive.

Typus: **Antarctica**, King George Island, Fildes Region, obtained from soil, Jan. 2017, *T. Zhang* (**holotype** CPCC 300077^{T} preserved in a metabolically inactive state, culture ex-type CBS 18357= P78733).

Glaciozyma ellipsoidea T. Zhang & J.J. Feng, ***sp. nov.*** MB 858799. Fig. 18.

Etymology: The scientific epithet *ellipsoidea* refers to the ellipsoidal shape of vegetative cells by microscopic observation.

Culture characteristics: After 7 d in YM broth at 12 °C, a sediment is formed. After 28 d in YM broth at 12 °C, a sediment and a ring with pellicle can be observed, the upper half part of the broth is turbid. After 7 d on YM agar at 12 °C, cells are long ellipsoidal to clavate or fusiform, 8.2–13.6 × 2.6–4.6 µm in size, occurring mainly single or in pairs, occasionally in triple, in quadruple or in a short chain constituted by several vegetative yeast cells, budding is polar. After 28 d on YM agar at 12 °C, the colonies are white to slightly yellowish white, butyrous, smooth, ridged, and wrinkled. The margin is entire, occasionally wrinkled or tassel-like. Pseudohyphae can be observed in the Dalmau plate culture on CMA at 12 °C after 2 wk, while true hyphae cannot be observed. Sexual reproduction cannot be observed on CMA, MEA, PDA, SYA, or YM agar.

Physiological characteristics: All the following assimilation and related tests were conducted at 12 °C. Fermentation is negative. The following sole carbon compounds can be assimilated: Glucose, sucrose, L-arabinose (delayed and weak), L-rhamnose, N-acetyl-D-glucosamine, D-mannitol, raffinose (delayed and weak), myo-inositol, inulin (weak), D-ribose (delayed), D-glucitol, glycerol, ethanol, D-Glucono-1,5-lactone, succinate, DL-lactate (delayed and weak), D-gluconate (delayed), erythritol, ribitol, maltose (delayed), citrate (weak), xylitol, D-galacturonate, DL-malic acid (delayed), L-arabinitol (delayed), D-glucuronate, propane-1,2-diol. The following sole carbon compounds cannot be assimilated: Melibiose, galactose, lactose, melezitose, trehalose, salicin, galactitol, methyl-α-D-glucoside, cellobiose, D-xylose, D-arabinose, L-sorbose, D-glucosamine, methanol, hexadecane, soluble starch, levulinic acid, butane-2,3-diol, isopropanol, arbutin. The following sole nitrogen compounds can be assimilated: Ammonium sulphate, L-lysine (delayed), ethylamine hydrochloride (delayed), cadaverine dihydrochloride (delayed), sodium nitrite, potassium nitrate. Growth in vitamin-free medium is positive. Growth is very weak or negative at 20 °C, but negative at 25 °C. Optimal growth temperature is between 4 °C and 15 °C. Growth in 0.01 % cycloheximide (w/v) is negative. Growth on 10 % NaCl + 5 % glucose medium (w/v) and 50 % glucose agar (w/w) are negative. Extracellular starch-like compounds are not produced. Urease reaction is positive. Diazonium Blue B reaction is positive.

Typus: **Spitsbergen** (Svalbard archipelago), Ny-Ålesund, obtained from soil, Jul. 2019, *T. Zhang* (**holotype** CPCC 300473^{T} preserved in a metabolically inactive state, culture ex-type CBS 18335 = ZT501).

Note: Physiologically, *Glaciozyma ellipsoidea* differs from *Glaciozyma elongata* in the ability to assimilate sucrose, L-arabinose, D-mannitol, myo-inositol, D-glucitol, maltose, citrate, xylitol, L-arabinitol and propane-1,2-diol.

Chioneozyma T. Zhang & J.J. Feng, ***gen. nov.*** MB 858800.

Etymology: The genus name refers to Chione, the goddess of snow and winter in ancient Greek mythology.

The genus is proposed according to the circumscription of strain CPCC 300339 and CPCC 300299 in the seven-gene phylogeny with additional strains CPCC 300081, CPCC 300302, CPCC 300308, CPCC 300309, CPCC

300310, CPCC 300493 and CPCC 300500 in the concatenated ITS-D1/D2 tree. This genus is a new member of *Kriegeriaceae*. Morphologically, *Chioneozyma* differs from its relative *Phenoliferia* in the colour of the colony. Physiologically, *Chioneozyma* differs from *Phenoliferia* in the ability to assimilate ethanol as a sole carbon source.

The colonies are mainly cream to white or yellowish white, butyrous, and smooth. Budding cells present and budding is polar. Fermentation is negative. A single cell is mainly ovoid, ellipsoidal or fusiform. Pseudohyphae can be observed in *Chioneozyma fusiformis* the Dalmau plate. Sexual reproduction cannot be observed, but teliospores or teliospore-like structures can be observed in some strains.

Type species: *Chioneozyma ovata* T. Zhang & J.J. Feng

Chioneozyma ovata T. Zhang & J.J. Feng, ***sp. nov.*** MycoBank MB 858801. Fig. 19.

Etymology: The scientific epithet *ovata* refers to the ovoid morphology of the cells by microscopic observation.

Culture characteristics: After 7 d in YM broth at 15 °C, a sediment is formed. After 28 d in YM broth at 15 °C, a sediment and a weak ring can be observed. After 7 d on YM agar at 15 °C, cells are ovoid to ellipsoidal, occasionally clavate, 6.9–9.3 × 3.3–5.2 µm in size, occurring mainly single or in pairs, occasionally in triple or in quadruple, budding is polar. After 28 d on YM agar at 15 °C, the colony is cream or white to slightly yellowish white, butyrous, smooth, and flat. The margin is entire. Pseudohyphae or true hyphae cannot be observed in the Dalmau plate culture on CMA at 15 °C. Sexual reproduction cannot be observed on CMA, MEA, PDA, SYA, or YM agar, but teliospores with germinated aseptate or septate hyphae can be observed on CMA and YM agar after 3 wk at 15 °C in strain CPCC 300081 and CPCC 300302. Teliospores subglobose to ovoid or ellipsoidal, 6–7 µm in width and 8–10 µm in length.

Physiological characteristics: All the physiological tests were conducted at 15 °C. Fermentation is negative. The following sole carbon compounds can be assimilated: Glucose, melibiose (sometimes delayed), sucrose,

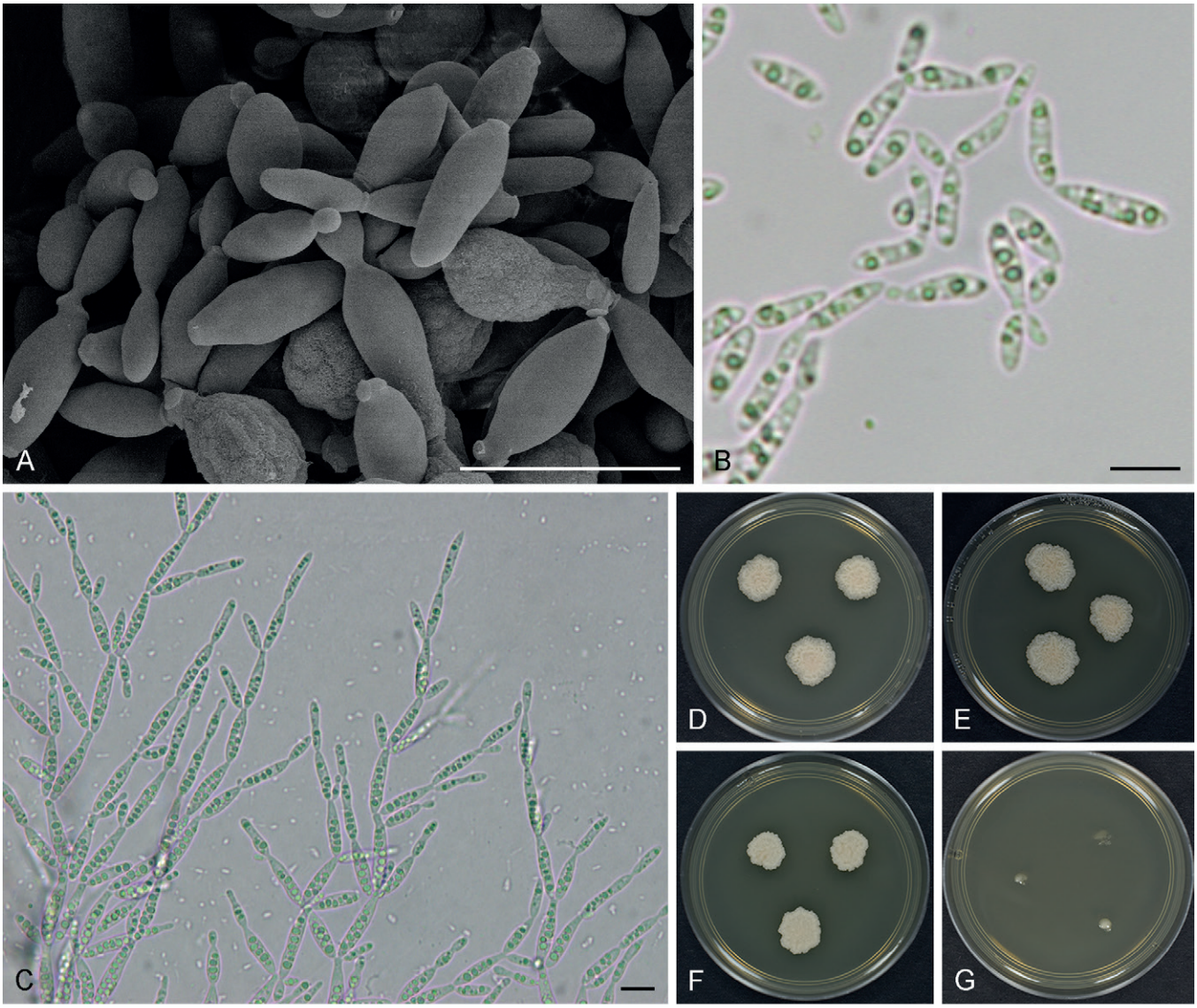

Fig. 18. *Glaciozyma ellipsoidea* CPCC 300473^{T}. **A.** SEM image of vegetative cells grown in YM broth after 6 d at 12 °C. **B.** Light microscopy image of vegetative cells grown on YM agar after 7 d at 12 °C. **C.** Pseudohyphae in the Dalmau plate culture on CMA at 12 °C after 2 wk. **D–G.** Views of colonies on YM agar at 4, 10, 15, and 20 °C after 4 wk. Scale bars = 10 µm.

melezitose, trehalose (sometimes delayed), salicin (variable), L-arabinose (variable), L-rhamnose (delayed and weak or weak), D-mannitol (variable), cellobiose (variable), raffinose, D-xylose (delayed or delayed and weak), D-arabinose (variable), L-sorbose (delayed and weak or weak), inulin (variable), D-ribose (delayed or delayed and weak), D-glucitol (delayed or weak), ethanol, D-Glucono-1,5-lactone (sometimes delayed), succinate (delayed or delayed and weak or weak), D-gluconate, ribitol (sometimes delayed), citrate (variable), xylitol, D-galacturonate (delayed or delayed and weak), arbutin (sometimes weak), L-arabinitol (sometimes weak), D-glucuronate (delayed or delayed and weak). The following sole carbon compounds cannot be assimilated: Galactose, lactose, galactitol, N-acetyl-D-glucosamine, methyl-α-D-glucoside, myo-inositol, D-glucosamine, glycerol, methanol, DL-lactate, hexadecane, erythritol, maltose, soluble starch, levulinic acid, butane-2,3-diol, isopropanol, DL-malic acid, propane-1,2-diol. The following sole nitrogen compounds can be assimilated: Ammonium sulphate, L-lysine (sometimes delayed), ethylamine hydrochloride, cadaverine dihydrochloride, potassium nitrate. The following sole nitrogen compound cannot be assimilated: Sodium nitrite. Growth in vitamin-free medium is positive. Growth is negative or weak at 25 °C, but negative at 28 °C. Optimal growth temperature is between 4 °C and 15 °C. Growth in 0.01 % cycloheximide (w/v) is negative. Growth on 10 % NaCl + 5 % glucose medium (w/v) and 50 % glucose agar (w/w) are negative. Extracellular starch-like compounds are not produced. Urease reaction is positive. Diazonium Blue B reaction is positive.

Typus: **Antarctica**, King George Island, Fildes Region, obtained from soil, Jan. 2017, *T. Zhang* (**holotype** CPCC 300339^{T} preserved in a metabolically inactive state, culture ex-type CBS 18339 = ZT113).

Chioneozyma fusiformis J.J. Feng & T. Zhang, ***sp. nov.*** MB 858802. Fig. 20.

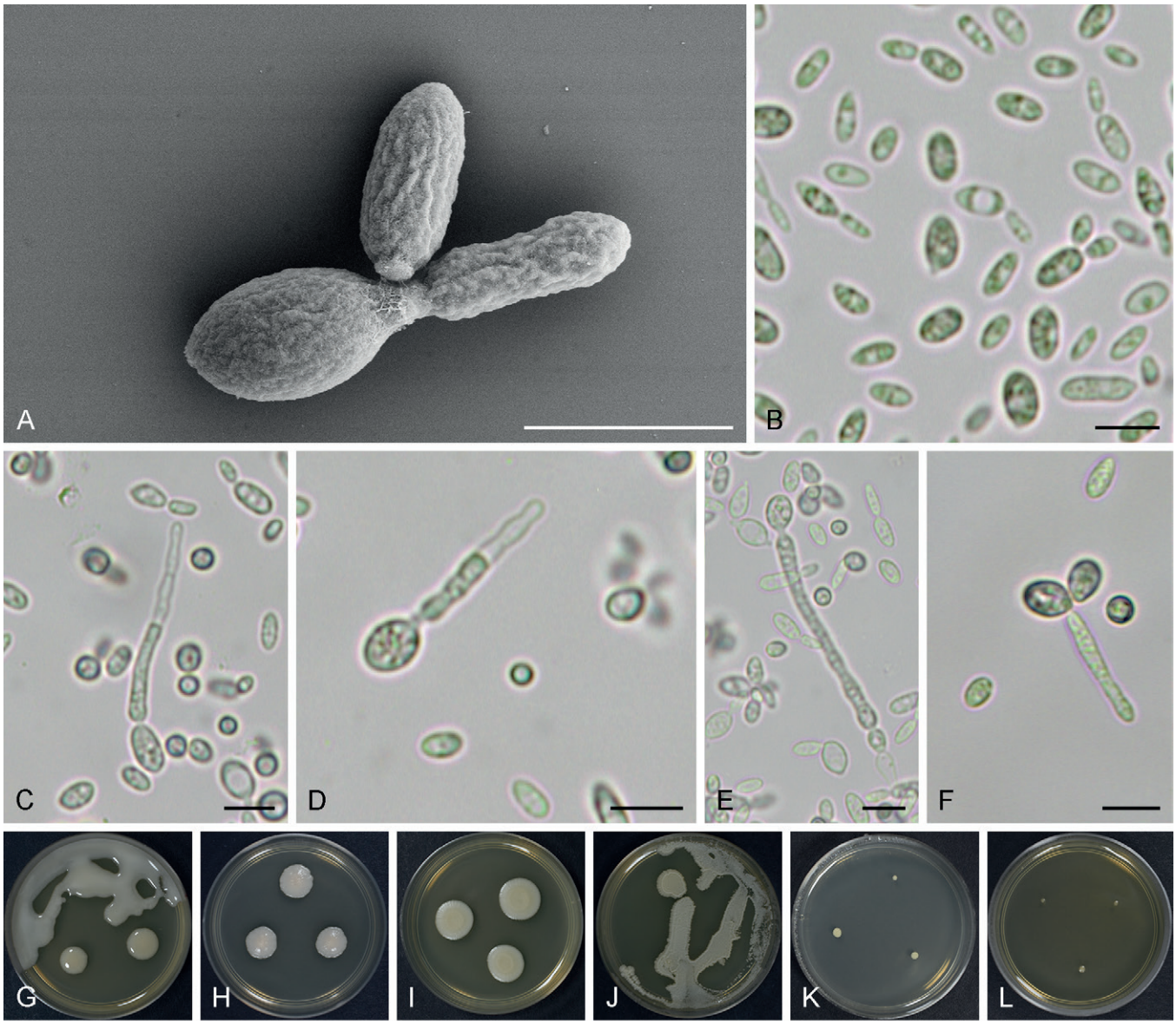

Fig. 19. *Chioneozyma ovata*. **A.** SEM image of vegetative cells grown in YM broth after 6 d at 12 °C (CPCC 300339^{T}). **B.** Light microscopy image of vegetative cells grown on YM agar after 7 d at 15 °C (CPCC 300339^{T}). **C, D.** Teliospores with hyphae on YM agar at 15 °C after 3 wk (CPCC 300081). **E.** Teliospores with hyphae on YM agar at 15 °C after 3 wk (CPCC 300302). **F.** Teliospores with hyphae on CMA at 15 °C after 3 wk (CPCC 300302). **G–L.** Views of colonies on YM agar at 4, 10, 15, 20, 25, and 28 °C after 4 wk (CPCC 300339^{T}). Scale bars: A = 5 µm; B–F = 10 µm.

Etymology: The scientific epithet *fusiformis* refers to the fusiform shape of cells by microscopic observation.

Culture characteristics: After 7 d in YM broth at 15 °C, a sediment is formed. After 28 d in YM broth at 15 °C, a sediment and a very weak ring can be observed. After 7 d on YM agar at 15 °C, cells are fusiform to ellipsoidal, 10.2–14.5 × 3.1–5.2 µm in size, occurring mainly in single, occasionally in pairs or in triple, budding is polar. After 28 d on YM agar at 15 °C, the colonies are cream or white to slightly yellowish white, butyrous, smooth, and flat. The margin is entire. Pseudohyphae can be observed in the Dalmau plate culture on CMA at 15 °C after 7 d, true hyphae cannot be observed. Sexual reproduction cannot be observed on CMA, MEA, PDA, SYA, or YM agar, but teliospores with germinated hyphae can be observed on PDA after 5 wk at 15 °C in strain CPCC 300309 without the isolation of mating. Teliospores terminal, globose or subglobose to pyriform, 10–11 µm in width and 11–14 µm in length. Occasionally inflated vegetative yeast cells or hyphae may develop directly from different sites of a teliospore simultaneously. Additionally, elongated septate hyphae derived from vegetative yeast cells can be observed on YM agar after 3–5 wk at 15 °C in strain CPCC 300310.

Physiological characteristics: All the physiological tests were conducted at 15 °C. Fermentation is negative. The following sole carbon compounds can be assimilated: Glucose, melibiose (variable), galactose (variable), sucrose (variable), melezitose (variable), trehalose (sometimes delayed), salicin (variable), L-arabinose (delayed or delayed and weak or weak), L-rhamnose (delayed or delayed and weak or weak), galactitol (variable), methyl-α-D-glucoside (variable), D-mannitol (sometimes delayed), raffinose (variable), D-xylose (sometimes delayed), D-arabinose (variable), L-sorbose (variable), inulin (variable), D-ribose (sometimes delayed or delayed and weak), D-glucitol (variable), glycerol (variable), ethanol (sometimes delayed), D-Glucono-1,5-lactone, succinate (variable), D-gluconate, ribitol, citrate (variable), xylitol (sometimes delayed), D-galacturonate (variable), arbutin (variable), L-arabinitol (sometimes delayed), D-glucuronate (weak). The following sole carbon compounds cannot be assimilated: Lactose, N-acetyl-D-glucosamine, cellobiose, myo-inositol, D-glucosamine, methanol, DL-lactate, hexadecane, erythritol, maltose, soluble starch, levulinic acid, butane-2,3-diol, isopropanol, DL-malic acid, propane-1,2-diol. The following sole nitrogen compounds can be assimilated: Ammonium sulphate, L-lysine (sometimes

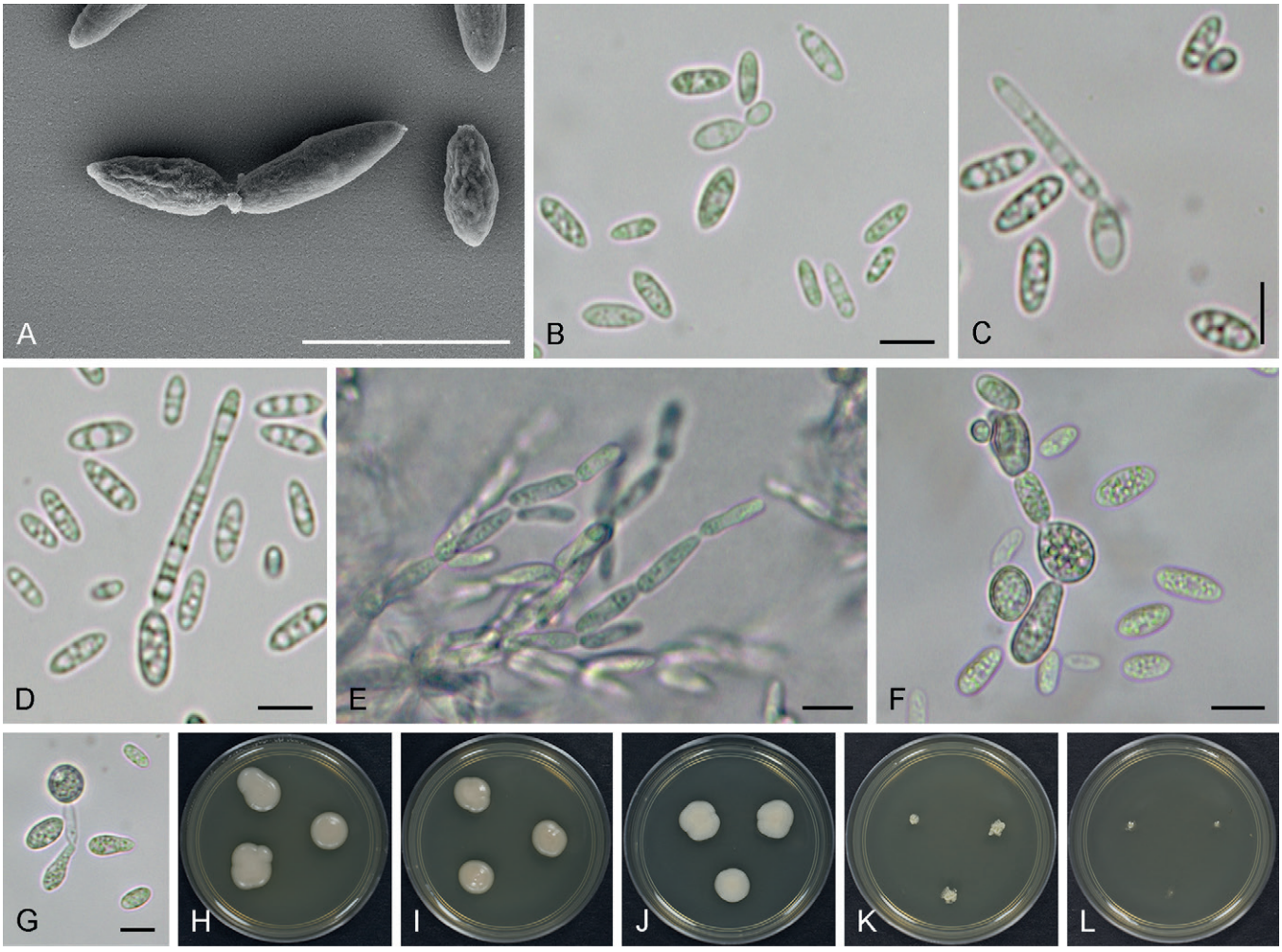

Fig. 20. *Chioneozyma fusiformis*. **A.** SEM image of vegetative cells grown in YM broth after 4 d at 12 °C (CPCC 300299^{T}). **B.** Light microscopy image of vegetative cells grown on YM agar after 7 d at 15 °C (CPCC 300299^{T}). **C.** Transversely septate hyphae on YM agar at 15 °C after 3 wk (CPCC 300310). **D.** Transversely septate hyphae on YM agar at 15 °C after 5 wk (CPCC 300310). **E.** Pseudohyphae in the Dalmau plate culture on CMA at 15 °C after 7 d (CPCC 300309). **F**, **G.** Teliospores with vegetative yeast cells or hyphae on PDA at 15 °C after 5 wk (CPCC 300309). **H–L.** Views of colonies on YM agar at 4, 10, 15, 20, and 25 °C after 4 wk (CPCC 300299^{T}). Scale bars = 10 µm.

delayed), ethylamine hydrochloride, sodium nitrite (variable), cadaverine dihydrochloride, potassium nitrate. Growth in vitamin-free medium is positive. Growth is negative at 25 °C. Optimal growth temperature is between 4 °C and 15 °C. Growth in 0.01 % cycloheximide (w/v) is negative. Growth on 10 % NaCl + 5 % glucose medium (w/v) and 50 % glucose agar (w/w) are negative. Extracellular starch-like compounds are not produced. Urease reaction is positive. Diazonium Blue B reaction is positive.

Typus: **Antarctica**, King George Island, Fildes Region, obtained from lichen, Jan. 2017, *T. Zhang* (**holotype** CPCC 300299^{T} preserved in a metabolically inactive state, culture ex-type CBS 18340 = P76083).

Note: *Chioneozyma fusiformis* shares similar assimilation profiles with *Chioneozyma ovata,* but the ability to assimilate melibiose as sole carbon compound is significantly weaker than that of *Chioneozyma ovata*, the size and shape of vegetative yeast cells are different as well.

Yunzhangia cylindrica T. Zhang & J.J. Feng, ***sp. nov.*** MB 843913. Fig. 21.

Etymology: The scientific epithet *cylindrica* refers to the shape of vegetative cells by microscopic observation.

Culture characteristics: After 7 d in YM broth at 15 °C, a sediment is formed. After 28 d in YM broth at 15 °C, a sediment and a partial ring can be observed. After 7 d on YM agar at 15 °C, cells are mainly cylindrical or ellipsoidal, occasionally subglobose to ovoid, 4.8–6.8 × 2.3–3.5 µm in size, occurring mainly in single, occasionally in pairs, in quadruple or in a short chain with several vegetative yeast cells, budding is polar. After 28 d on YM agar at 15 °C, the colonies are tan to greyish or yellowish white, butyrous, smooth, flat, and somewhat glistening. The margin is entire. Pseudohyphae or true hyphae cannot be observed in the Dalmau plate culture on CMA at 15 °C. Sexual reproduction cannot be observed on CMA, MEA, PDA, SYA, or YM agar, but long aseptate multinucleate hyphae can be observed after 2 wk on PDA at 15 °C.

Physiological characteristics: All the following assimilation and related tests were conducted at 15 °C. Fermentation is negative. The following sole carbon compounds can be assimilated: Glucose, galactose (delayed and weak), trehalose (delayed), D-mannitol (delayed and weak), D-glucitol (weak), D-Glucono-1,5-lactone, succinate. The following sole carbon compounds cannot be assimilated: Melibiose, sucrose, lactose, melezitose, salicin, L-arabinose, L-rhamnose, galactitol, N-acetyl-D-glucosamine, methyl-α-D-glucoside, cellobiose, raffinose, D-xylose, myo-inositol, D-arabinose, L-sorbose, inulin, D-ribose, D-glucosamine, glycerol, ethanol, methanol, DL-lactate, D-gluconate, hexadecane, erythritol, ribitol, maltose, citrate, soluble starch, xylitol, levulinic acid, butane-2,3-diol, D-galacturonate, isopropanol, arbutin, DL-malic acid, L-arabinitol, D-glucuronate, propane-1,2-diol.

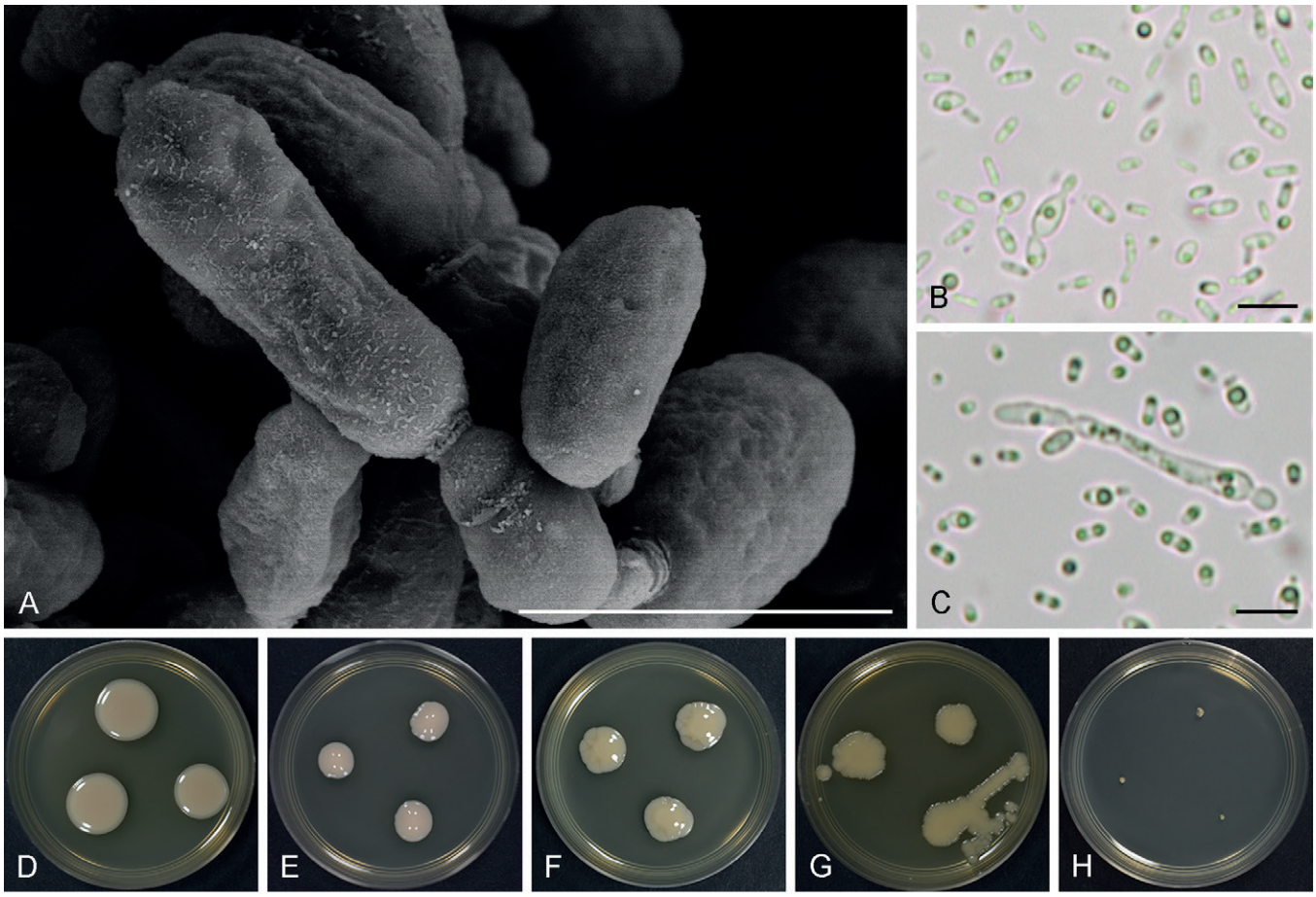

Fig. 21. *Yunzhangia cylindrica* CPCC 300385^{T}. **A.** SEM image of vegetative cells grown in YM broth after 6 d at 12 °C. **B.** Light microscopy image of vegetative cells grown on YM agar after 7 d at 15 °C. **C.** Long aseptate multinucleate hyphae-like structure on PDA at 15 °C after 2 wk. **D**–**H.** Views of colonies on YM agar at 4, 10, 15, 20, and 25 °C after 4 wk. Scale bars: A = 4 µm; B, C = 10 µm.

The following sole nitrogen compounds can be assimilated: Ammonium sulphate, L-lysine, ethylamine hydrochloride (delayed and weak), cadaverine dihydrochloride (delayed), potassium nitrate. The following sole nitrogen compound cannot be assimilated: Sodium nitrite. Growth in vitamin-free medium is negative. Growth is negative at 25 °C. Optimal growth temperature is between 4 °C and 15 °C. Growth in 0.01 % cycloheximide (w/v) is negative. Growth on 10 % NaCl + 5 % glucose medium (w/v) and 50 % glucose agar (w/w) are negative. Extracellular starch-like compounds are not produced. Urease reaction is positive. Diazonium Blue B reaction is positive.

Typus: **Spitsbergen** (Svalbard archipelago), Ny-Ålesund, obtained from vascular plant, Jul. 2019, *T. Zhang* (**holotype** CPCC 300385^{T} preserved in a metabolically inactive state, culture ex-type CBS 18350 = ZT305).

Notes: Physiologically, *Yunzhangia cylindrica* differs from its closest relative *Yunzhangia sonckii* in the inability to assimilate D-xylose, L-sorbose, glycerol, and DL-lactate. The maximal growth temperature of *Yunzhangia cylindrica* is also lower than that of *Yunzhangia sonckii* (Hopsu-Havu *et al.* 1978).

Fellozyma antarctica J.J. Feng & T. Zhang, ***sp. nov.*** MB 843883. Fig. 22.

Etymology: The scientific epithet antarctica refers to the geographical origin from which the species was first described.

Culture characteristics: After 7 d in YM broth at 15 °C, a sediment and a ring are formed. After 28 d in YM broth at 15 °C, a sediment and a ring with partial pellicle can be observed. After 7 d on YM agar at 15 °C, cells are long ellipsoidal to clavate or fusiform, 7.3–11.0 × 2.2–3.8 µm in size, occurring mainly single or in pairs, occasionally in a short chain with three to four vegetative yeast cells, budding is polar. After 28 d on YM agar at 15 °C, the colonies are yellowish white to yellow, butyrous, smooth, and flat. The margin is entire. Primitive pseudohyphae can be observed on YM agar and in the Dalmau plate culture on CMA at 15 °C after 7 d, true hyphae cannot be observed. Sexual reproduction cannot be observed on CMA, MEA, PDA, SYA, or YM agar.

Physiological characteristics: All the following assimilation and related tests were conducted at 15 °C. Fermentation is negative. The following sole carbon compounds can be assimilated: Glucose, melibiose (variable), galactose (weak), sucrose, lactose (delayed and weak or weak), melezitose, trehalose (sometimes delayed), salicin (weak), L-arabinose (variable), galactitol (delayed and weak), methyl-α-D-glucoside (variable), D-mannitol, cellobiose (delayed), raffinose (weak), D-xylose (delayed and weak

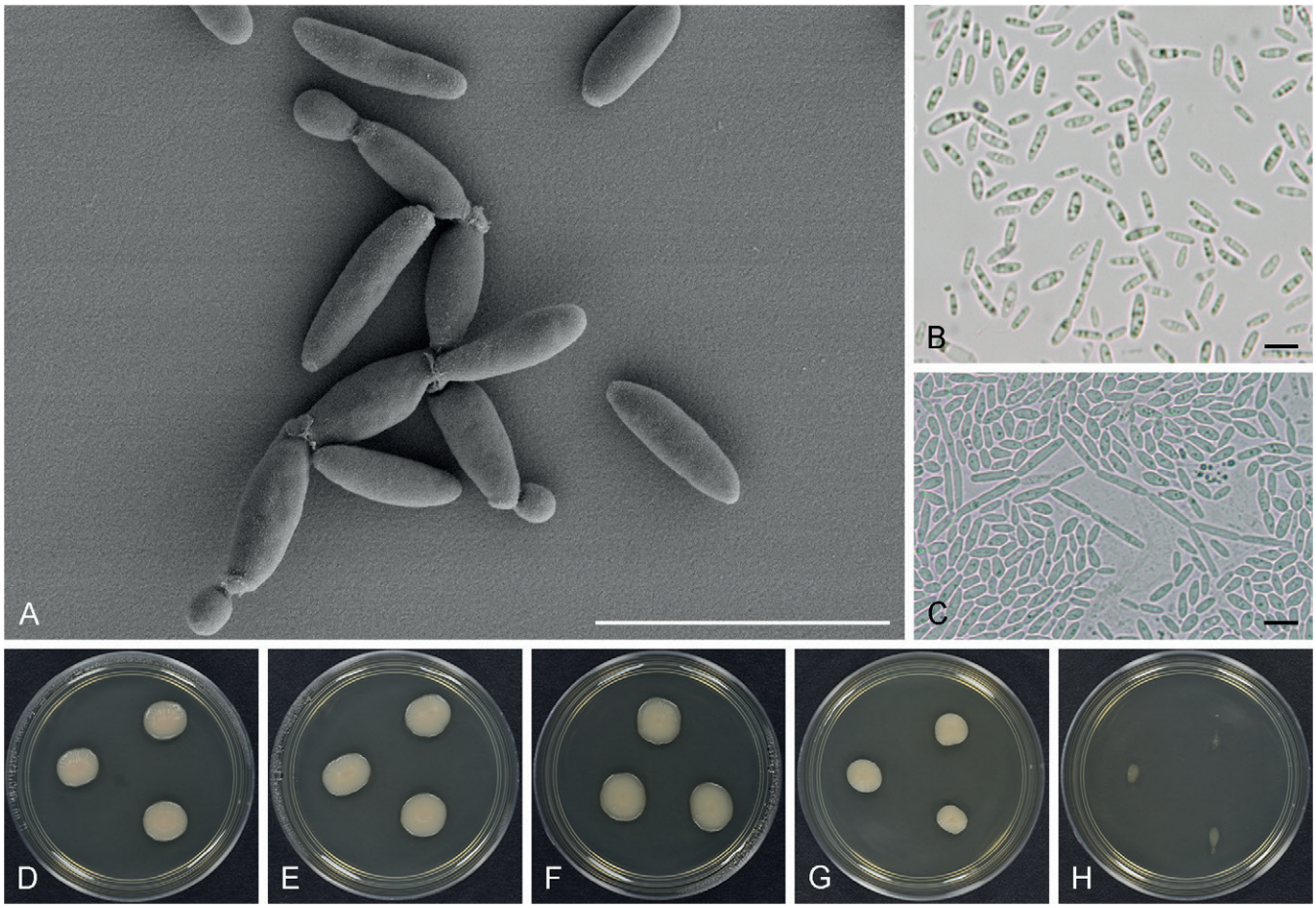

Fig. 22. *Fellozyma antarctica* CPCC 300301^{T}. **A.** SEM image of vegetative cells grown in YM broth after 4 d at 12 °C. **B.** Light microscopy image of vegetative cells grown on YM agar after 7 d at 15 °C. **C.** Primitive pseudohyphae in the Dalmau plate culture on CMA at 15 °C after 7 d. **D–H.** Views of colonies on YM agar at 4, 10, 15, 20, and 25 °C after 4 wk. Scale bars = 10 µm.

or weak), myo-inositol (delayed or weak), D-arabinose (variable), L-sorbose (delayed and weak or weak), D-glucitol (delayed), glycerol (delayed or weak), ethanol (sometimes delayed), D-Glucono-1,5-lactone, succinate, DL-lactate (weak), D-gluconate, ribitol (delayed and weak), maltose (weak), citrate, xylitol (delayed or weak), levulinic acid (delayed and weak or weak), D-galacturonate (delayed), DL-malic acid (variable), D-glucuronate. The following sole carbon compounds cannot be assimilated: L-rhamnose, N-acetyl-D-glucosamine, inulin, D-ribose, D-glucosamine, methanol, hexadecane, erythritol, soluble starch, butane-2,3-diol, isopropanol, arbutin, L-arabinitol, propane-1,2-diol. The following sole nitrogen compounds can be assimilated: Ammonium sulphate, L-lysine, ethylamine hydrochloride, cadaverine dihydrochloride, potassium nitrate. The following sole nitrogen compound cannot be assimilated: Sodium nitrite. Growth in vitamin-free medium is delayed. Growth is negative at 25 °C. Optimal growth temperature is between 4 °C and 15 °C. Growth in 0.01 % cycloheximide (w/v) is negative. Growth on 10 % NaCl + 5 % glucose medium (w/v) and 50 % glucose agar (w/w) are negative. Extracellular starch-like compounds are not produced. Urease reaction is positive. Diazonium Blue B reaction is positive.

Typus: **Antarctica**, King George Island, Fildes Region, obtained from lichen, Jan. 2017, *T. Zhang* (**holotype** CPCC 300301^{T} preserved in a metabolically inactive state, culture ex-type CBS 18331 = P7608C).

Notes: Physiologically, *Fellozyma antarctica* differs from its relative *Fellozyma inositophila* in the ability to assimilate galactose, lactose, salicin, galactitol, cellobiose, raffinose, D-xylose, L-sorbose, D-Glucono-1,5-lactone, DL-lactate, ribitol, L-lysine and in the inability to assimilate sodium nitrite. The maximal growth temperature of *Fellozyma antarctica* was lower than that of *Fellozyma inositophila* (Nakase & Suzuki 1987).

DISCUSSION

The diversity of yeast species in various polar habitats – including soils, macroalgae, plants, lichens, bryophytes, and meltwater biofilms in Antarctica, as well as glaciers and coastal environments in the Arctic – has been documented in previous studies (Connell *et al.* 2008, Santiago *et al.* 2017, Duarte *et al.* 2016, Ferreira *et al.* 2019, Butinar *et al.* 2007, 2011). Despite these valuable contributions, a comprehensive study integrating diverse habitats from both the Arctic and Antarctica remains lacking. Our work addresses this gap by revealing the extensive diversity and geographical distribution of yeast species in these regions, suggesting their broader ecological implications and potential for novel biotechnological applications, as discussed below.

In the Arctic, we have identified several yeast species for the first time, including *Candida davisiana*, *Cystobasidium raffinophilum*, *Cryolevonia giraudoae*, *Dioszegia antarctica*, *Dioszegia rishiriensis*, *Glaciozyma martinii*, *Phenoliferia psychrophila*, *Mrakia niccombsii*, *Mrakia stelviica*, *Heterocephalacria sinensis*, *Naganishia nivalis*, *Piskurozyma yama*, *Phaeotremella lacus*, *Filobasidium stepposum*, *Holtermanniella nyarrowii*, and *Tremella indecorata*. Similarly, in Antarctica, we have documented the first records of *Candida railenensis*, *Meira plantarum*, *Cryolevonia schafbergensis*, *Psychromyces glacialis*, *Curvibasidium nothofagi*, *Slooffia velesii*, *Leucosporidium himalayensis*, *Rhodotorula taiwanensis*, *Mrakia hoshinonis*, *Naganishia uzbekistanensis*, *Piskurozyma yama*, and *Kwoniella ovata*. This study demonstrates that many yeast species previously identified in non-polar habitats are also present in polar regions.

Remarkably, eleven species identified in this study were recently described, including *Cryolevonia giraudoae*, *Cryolevonia schafbergensis*, *Cystobasidium raffinophilum*, *Heterocephalacria sinensis*, *Kwoniella ovata*, *Leucosporidium himalayensis*, *Meira plantarum*, *Mrakia hoshinonis*, *Mrakia stelviica*, *Naganishia nivalis*, and *Psychromyces glacialis*. Specifically, the genus *Cryolevonia*, established in 2020, comprises two species: *Cryolevonia schafbergensis*, isolated from permafrost soil in the Swiss Alps and melting sea ice on Baffin Island (Canada), and *Cryolevonia giraudoae*, discovered in glacial ice in Argentina's Patagonia and marine ice in the Antarctic Peninsula (de Garcia *et al.* 2020, Pontes *et al.* 2020). *Psychromyces* represents a monotypic genus containing the single species *P. glacialis*, which has been reported from Svalbard and Greenland (Perini *et al.* 2021). *Mrakia hoshinonis* and *Mrakia stelviica* were respectively found in glacial sediments in Canada's Ellesmere Island and in Italy's Alps, respectively (Tsuji *et al.* 2019a, Turchetti *et al.* 2020). *Naganishia nivalis* was isolated from snow in the Italian Alps (Kachalkin *et al.* 2019). Additionally, *Heterocephalacria sinensis*, *Cystobasidium raffinophilum*, *Kwoniella ovata*, and *Meira plantarum* were associated with various substrates in China (Li *et al.* 2019, 2020, 2021), highlighting the growing interest in uncovering new yeast taxa.

Overall, this study identified 98 yeast species, 34 of which were found in both the Arctic and Antarctic regions. Similar fungal communities in both polar regions have been revealed through high-throughput sequencing, as highlighted by Cox *et al.* (2016). This supports the hypothesis, proposed by Finlay (2002), Foissner (2006), and Sato *et al.* (2012), of a wide cosmopolitan distribution of fungi and other free-living microorganisms. Anthropogenic activities may influence the distribution of yeast species, as suggested by Samarasinghe *et al.* (2021). However, the global distribution patterns of most yeast species remain largely unexplored, highlighted by Boekhout *et al.* (2022), due to the challenges of conducting comprehensive worldwide sampling.

In terms of habitat, a significant number of the novel yeast species identified were found in lichens, soils, freshwater, and vascular plants, as listed in Table 2. These habitats are likely to serve as vast reservoirs for numerous yet-to-be-discovered yeast species. For example, several novel psychrophilic species within the *Camptobasidiaceae* family, including new genera such as *Skadia* and *Xuelongia*, have been isolated from freshwater sources in the Arctic. This suggests that many additional yeasts that remain undiscovered may inhabit the freshwater of polar regions, warranting further exploration and study. Historically, soil has been an important habitat for the identification of new yeast taxa; for instance, various new *Mrakia* species have been isolated from Antarctic soil (di Menna 1966, Xin & Zhou 2007, Thomas-Hall *et al.* 2010). Several studies revealed at least 427 lichens species in Antarctica (Øvstedal & Lewis Smith 2001) and 752 species

in Svalbard (Øvstedal *et al.* 2009), which offer a unique "lichensphere" that serves as a protective microhabitat for colonizing organisms, including yeasts, in extreme conditions (Santiago *et al.* 2015). The study of yeasts within lichen thalli, though limited, has shown a high diversity of basidiomycetous yeasts, further emphasizing the ecological importance of lichens in hosting novel yeast lineages (Cometto *et al.* 2022).

Certain polar yeast species have developed mechanisms to adapt to extreme environmental factors, such as low temperatures, oligotrophic conditions, strong radiation, and freeze-thaw cycles, making them exceptional resources for discovering new functions and metabolic products. Lee *et al.* (2010) isolated a yeast strain with ice-binding activity, *Leucosporidium* sp. AY30, from freshwater in the Arctic. This strain demonstrated ice-etching activity and recrystallization inhibition activity at temperatures between 0–15 °C, and its ice-binding protein (IBP) was identified (Lee *et al.* 2012). IBPs from polar yeasts are crucial for the cryogenic preservation of biological specimens across animals, plants, organs, and cells, and have applications in the food and healthcare industries. Khan *et al.* (2019) isolated an antifreeze peptide (Afp1m) from the Antarctic yeast *Glaciozyma antarctica*, which exhibited no damage to the epidermis, dermis, and subcutaneous areas of rat skin grafts, indicating its potential for cryopreservation of transplant organs. Moreover, polar yeasts are capable of synthesizing cold-active enzymes with high catalytic efficiency, which possess significant research and application value (Kim *et al.* 2014). From glacial sediments in the Ny-Ålesund Region (High Arctic), 132 psychrophilic yeast strains were isolated, showing the capability to produce cold-active lipases, proteases, pectinases, cellulases, and amylases (Pathan *et al.* 2010). A lipase secreted by the yeast *Mrakia blollopis* from Antarctic soil exhibited significant thermal stability and pH stability (Tsuji *et al.* 2013), and such lipases are considered excellent methods for synthesizing single isomer chiral drugs through hydrolysis, ester exchange, or aminolysis reactions (Gotor-Fernandez *et al.* 2006).

In summary, this study on yeast diversity in the Arctic and Antarctica unveils a remarkable variety of species, emphasizing the need for further exploration of these ecosystems, especially in light of climate change. The shared species across these distinct habitats suggest ecological connections and provide potential insights into the origins of extremophiles. Future research should prioritize employing some innovative techniques, such as culturomics (Li *et al.* 2023), and enrichment strategies (Raudabaugh & Aime 2023), to acquire a broader range of yeast species, thus facilitating their conservation and exploring their biotechnological potential. Although our primary focus was to investigate the overall diversity across various habitats, we recognize that temporal variations in yeast communities could offer valuable insights, particularly in the context of rapidly changing climatic conditions. Long-term monitoring of microbial communities is essential for understanding how environmental changes – such as temperature fluctuations, precipitation patterns, and habitat alterations – impact community structure and function. Future studies could address this by adopting a longitudinal sampling strategy, maintaining consistent efforts across years and locations, to examine potential correlations between yeast community shifts and climatic factors.

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Supplementary material

Fig. S1. A. Global map indicating the geographical locations of the Ny-Ålesund region (Svalbard Archipelago, Arctic) and the Fildes region (King George Island, Antarctica). **B–D.** Detailed maps of the Ny-Ålesund region, Svalbard Archipelago (Arctic). **E–G.** Detailed maps of the Fildes region, King George Island (Antarctica).

Fig. S2. Phylogenetic tree inferred using the combined sequences of LSU rDNA D1/D2 domains and ITS region (including 5.8S rDNA), showing the phylogenetic positions of new taxa (in bold) within genera *Pseudotremella, Genolevuria,* and *Pricozyma*. The tree was constructed using maximum likelihood analysis, and bootstrap values over 50 % from 1000 replicates are shown. Scale bar: 0.05 substitutions per nucleotide position.

Fig. S3. Phylogenetic tree inferred using the combined sequences of LSU rDNA D1/D2 domains and ITS region (including 5.8S rDNA), showing the phylogenetic positions of new taxa (in bold) within genus *Dioszegia*. The tree was constructed using maximum likelihood analysis, and bootstrap values over 50 % from 1000 replicates are shown. Scale bar: 0.03 substitutions per nucleotide position.

Fig. S4. Phylogenetic tree inferred using the combined sequences of LSU rDNA D1/D2 domains and ITS region (including 5.8S rDNA), showing the phylogenetic positions of new taxa (in bold) within genera *Phaeotremella* and *Xiangyanghongia*. The tree was constructed using maximum likelihood analysis, and bootstrap values over 50 % from 1000 replicates are shown. Scale bar: 0.05 substitutions per nucleotide position.

Fig. S5. Phylogenetic tree inferred using the combined sequences of LSU rDNA D1/D2 domains and ITS region (including 5.8S rDNA), showing the phylogenetic positions of new taxa (in bold) within genus *Piskurozyma*. The tree was constructed using maximum likelihood analysis, and bootstrap values over 50 % from 1000 replicates are shown. Scale bar: 0.05 substitutions per nucleotide position.

Fig. S6. Phylogenetic tree inferred using the combined sequences of LSU rDNA D1/D2 domains and ITS region (including 5.8S rDNA), showing the phylogenetic positions of new taxa (in bold) within genera *Chioneozyma*, *Fellozyma*, *Glaciozyma*, *Skadia*, and *Xuelongia*. The tree was constructed using maximum likelihood analysis, and bootstrap values over 50 % from 1000 replicates are shown. Scale bar: 0.05 substitutions per nucleotide position.

Fig. S7. Phylogenetic tree inferred using the combined sequences of LSU rDNA D1/D2 domains and ITS region (including 5.8S rDNA), showing the phylogenetic positions of new taxa (in bold) within genus *Yunzhangia*. The tree was constructed using maximum likelihood analysis, and bootstrap values over 50 % from 1000 replicates are shown. Scale bar: 0.04 substitutions per nucleotide position.

Table S1. Yeast species described as novel taxa isolated from Antarctica and the Arctic in previous studies.

Table S2. Primers used for amplification and sequencing in this study.

Table S3. Information on species, strains, and GenBank accession numbers used in the seven-gene phylogenetic analyses of *Tremellomycetes* (*Agaricomycotina*) in this study.

Table S4. Information on species, strains, and GenBank accession numbers used in the seven-gene phylogenetic analyses of *Microbotryomycetes* (*Pucciniomycotina*) in this study.

Table S5. Information on species, strains, GenBank accession numbers, and sources used in the two-gene phylogenetic analyses of *Tremellomycetes* (*Agaricomycotina*) in this study.

Table S6. Information on species, strains, GenBank accession numbers, and sources used in the two-gene phylogenetic analyses of *Microbotryomycetes* (*Pucciniomycotina*) in this study.